



Keratroides vulgaris (Friend)

The taxonomy, zoogeography and
aspects of the ecology of the terrestrial
amphipods (Amphipoda:Talitridae)
of Tasmania

by

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Except as stated herein, this dissertation
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JA Friend

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SUMMARY

Amphipods of the family Talitridae form an important part of the cryptozoa of Tasmanian forests. This terrestrial amphipod fauna comprises fifteen species, and twelve of these are described as new. The currently widely-used grouping of land amphipods into the genera *Orchestia* and *Talitrus* is considered unsatisfactory and consequently new genera are proposed for the Tasmanian species. A key for the identification of these species is provided.

The detailed distribution of each of these species is presented and discussed with respect to the environments present in Tasmania and their history. Four of the seven Tasmanian genera, but only one of the fifteen species, are found on the mainland of Australia. Examination of geological and paleo-climatic data leads to the suggestion that this situation is due to the particular conditions which prevailed on former land connections, during Tertiary and late Quaternary times.

The world distribution of terrestrial amphipods is examined in the light of local knowledge. A Gondwanaland radiation of the Talitroidea is suggested, and the proposal that supralittoral talitrids were not present in the Laurasian continents until the late Tertiary is advanced.

Ecological studies of land amphipods in Tasmania were focussed on the areas of niche partition and the dynamics of populations and their environment. All investigations were carried out at a site in wet sclerophyll forest in eastern Tasmania.

Two species, sympatric at the study site, were found to display a number of ecological differences which may explain their coexistence. *Keratroides vulgaris* appears to be a litter-dwelling, actively-colonizing species, while *K. angulosus* possesses morphological and behavioural attributes which apparently fit it better for its demonstrated existence at a lower level in the litter/soil profile.

Litter fall and decomposition was studied at the study site over 18 months. Annual litter fall was 9390 kg/ha, which is high compared with results from

studies in other Australian forests. While litter fell throughout the year, there was a distinct summer peak. Estimates of the rate of disappearance of litter indicated a low turnover time, approaching those found in forests in much warmer climates. The concentrations of several important nutrients in components of the newly-fallen litter and the forest floor at the study site were measured. Levels of most of these nutrients, especially phosphorus, proved higher than those found in other Australian forests.

The numbers and structures of populations of *K. vulgaris* and *K. angulosus* were also monitored for 18 months. High densities of both species were maintained throughout this time, reaching maxima of $2431/m^2$ and $6185/m^2$ respectively, in December 1977. Ovigerous females of both species were found almost exclusively between September and May, and photoperiod control of the winter resting stage is suggested. Both species displayed two-year life cycles and many individuals apparently bred during consecutive summers. Comparison of patterns of reproduction found in this and other populations of terrestrial talitrids reveals a wide diversity of strategies within this group.

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CHAPTER ONE

INTRODUCTION

Terrestrial amphipods are an important element of the leaf litter and soil fauna of the wetter forests of eastern Australia, both in terms of numbers (Sayce, 1909; Campbell and Gray, 1942; Clark, 1954; Sandell, 1977; Friend and Richardson, 1977) and in terms of their contribution to litter decomposition (Clark, 1954; Friend, 1975).

The group is widely distributed in tropical and southern hemisphere areas of the world (Hurley, 1968). Discounting known introductions, there are published records from Australia, New Guinea, New Zealand and its sub-antarctic islands, South Africa, Madagascar, India, Ceylon, Burma, Singapore, Indonesia, the Philippines, Japan, most major Pacific and Indian Ocean island groups, the Azores, Madeira, Canary Is., and Annobon I. Unpublished records from Jamaica, Haiti and Panama are cited by Hurley (1968), while an endemic species has also been found in Mexico (E.L. Bousfield, pers. comm.). The known distribution of this fauna is shown in Figure 4.1.

The importance of this cryptozoan group is certainly belied by the small amount of ecological literature devoted to it (see below). The lack of attention has been attributed to the absence of native land amphipods from much of the northern hemisphere, where most ecological research has been carried out (Friend and Richardson, 1977). While perhaps explaining the state of terrestrial amphipod ecology, this world distribution also presents an interesting zoogeographical problem, to which a comprehensive answer has not been provided. It is widely agreed that fully land-dwelling amphipods, which belong to the family Talitridae, arose from species similar to those commonly found on seashores (Bulycheva, 1957; Hurley, 1959, 1968; Bousfield, 1968; Wildish, 1979). Representatives of this supralittoral group, however, are present on seashores on all continents and on islands of both hemispheres, to about 60° latitude, north and south (Bulycheva, 1957). The problem, then, is to explain why terrestrial amphipods are so poorly represented in

the northern hemisphere, where supralittoral species are quite common.

In the course of a zoological survey by the present author and fellow honours students in 1974, it became obvious that there is a relatively rich and largely undescribed terrestrial amphipod fauna in Tasmania. It was also discovered that it is usual to find several species together in the forest floor. These findings invited research in two different, but not unrelated, directions.

Description of the land amphipod fauna was a definite priority; it is largely the lack of knowledge of cryptozoan groups which has discouraged ecological work on the Australian forest floor fauna (see below). The unsettled state of terrestrial talitrid taxonomy (Chapter 2) quickly became evident, as did the poor knowledge of this fauna in the rest of Australia. Tasmanian species apparently formed distinct groups within the taxa at present accepted by some as genera (Hurley, 1955, 1957, 1975a; Bulychева, 1957; Barnard, 1969) and these groups sometimes fell between the classical concepts of *Orchestia* and *Talitrus*. This taxonomic study rapidly assumed the proportions of a revision, so comparative material from other regions was acquired for study through both personal collecting and museum loans.

The other area of research stimulated by early findings concerns the co-occurrence of amphipod species. The means of coexistence of sympatric species has been the subject of many studies (review by Schoener, 1974). Amongst the cryptozoa, however, research along these lines has been less extensive, although these communities present particularly interesting problems because of the high numbers of species apparently coexisting (Anderson and Healey, 1972). The terrestrial amphipods show relatively little morphological divergence (Barnard, 1960) and apparently little feeding specialization (Hurley, 1968; Duncan, 1969; Friend, 1975) thus presenting a challenging area for study.

It has been stated that terrestrial amphipods are morphologically very similar to related shore-dwelling species (Hurley, 1968). The terrestrial environment, however, must present different problems to the animals living there, and different solutions must presumably be found. Reproduction is one area where these differences might be highlighted, and one where different strategies, by altering population dynamics, might have far-reaching effects in terms of the impact of populations on their environment. A study of the population dynamics and reproduction of two Tasmanian terrestrial species was carried out in order to assess these possibilities.

Studies by Clark (1954) and Friend (1975) suggested that land amphipods are quantitatively important in the initial breakdown of the annual litter fall. Madden *et al.* (1976) measured rates of litter fall and decomposition in wet sclerophyll forest sites of various ages, but theirs is the only Tasmanian study of these processes yet published. To gain some insight into the dynamic aspects of the environment of terrestrial amphipods, investigations were carried out into the rate and composition of litter fall and the rate of decomposition of litter at the site where amphipod populations were studied. These investigations also formed part of a broader study of the role of terrestrial amphipods in energy flow and nutrient dynamics at that site.

Arrangement

This dissertation is organized into two major parts. Part I concerns taxonomic and zoogeographic aspects of Tasmanian terrestrial amphipods. In Chapter 2, some preliminary taxonomic problems are stated while Chapter 3 is devoted to the main descriptive section, although a number of broad conclusions are drawn. The distribution of Tasmanian species is described in Chapter 4, and the information gained is used in an attempt to explain the global distribution of land amphipods.

Part II deals with several aspects of the ecology of some Tasmanian terrestrial amphipods. Studies were all carried out at a site in eastern Tasmania, which is described in detail in Chapter 5. As land amphipods are involved in litter decomposition, a holistic study of litter fall and decomposition was carried out, and is described in Chapter 6. In Chapter 7, means of coexistence of the two species most common at the site are investigated. Chapter 8 deals with a study of the population dynamics of these two species, and with reproductive strategies found amongst the supralittoral and terrestrial Talitridae. Two published articles and a recently-completed manuscript (yet to be submitted) which concern aspects of this thesis are included in the Appendix.

In the remainder of Chapter 1, the precise definition of "terrestrial amphipod" is discussed. The literature concerning the taxonomy of the Australian fauna is reviewed, together with the few non-taxonomic publications on the group.

Terrestrial Amphipoda.

There has been some discussion in the literature (Hurley, 1968; Wildish, 1979) about the use of the term "terrestrial" when referring to the habitat of some amphipods. It has occasionally been used erroneously with reference to those species which inhabit the supralittoral zone (*sensu* Stephenson and Stephenson, 1949) of the northern hemisphere (e.g. Dahl, 1946; Reid, 1947; Williamson, 1951a, 1951c). This usage has prompted the intro-

duction of more specific terms to refer to amphipods which are *bona fide* members of the litter fauna, living independently of water bodies and occurring away from the supralittoral zone. These terms include "truly terrestrial amphipod" (Stephensen, 1935a), "euterrestrial amphipod" (Tamura and Koseki, 1974) and "landhopper" (Chilton, 1909a; Smith, 1909; Bousfield, 1964). For the purposes of this study, the equivalent terms "terrestrial amphipod" (*sensu* Hurley, 1968), "land amphipod" and "landhopper" will be used for fully land-dwelling species, while "supralittoral" will be used to describe amphipods whose habitat is restricted to the vicinity of the high-water mark, most probably by ionic requisites (MacIntyre, 1954). As a rule, individual species found in each of these habitats are fairly rigorously excluded from the other. This has been found to be true in Tasmania; however, exceptions appear in the literature, and one of them (*Orchestia anomala* Chevreux) is discussed in Section 4.1.

While it has often been stated that only amphipods belonging to the family Talitridae have colonized the land (e.g. Bliss and Mantel, 1967; Bousfield, 1978), two interesting European records must be noted. Firstly, Bick (1958) refers to the occurrence of *Gammarus pulex fossarum* Koch in wet leaf litter beside streams in Hungary, and maintains that these animals are important in litter decomposition. While this constitutes participation in the forest ecosystem, this species is primarily aquatic, and it would appear, only leaves the stream when the litter is saturated, thus moving into an extension of its aquatic habitat. Secondly, Ghilarov et al., (1974) reported the presence of a previously unknown blind gammarid, *Niphargus talikadzei*, which was found commonly up to 10 cm deep in soil under alder thickets and in a tea plantation in the Kolkhidsk Depression, Russia. Groundwater was found at depths up to 120 cm. The extent to which this species is independent of water (as in Hurley, 1968) is not known, but its path towards a terrestrial existence clearly leads from a phreatic origin. This is in contrast to the migration through the supralittoral which has occurred in the Talitridae. All subsequent discussion of terrestrial

amphipods will concern members of this family only.

Taxonomic studies of Australian terrestrial amphipods

The first record of land amphipods in Australia was provided by Haswell (1880) who described *Talitrus sylvaticus* from New South Wales, noting that specimens had been found thirty miles inland. In 1881 he described *T. assimilis* from Tasmanian material and later (1882) listed both species (calling *T. assimilis* "*affinis*" by mistake) in his catalogue of sessile-eyed Crustacea of Australia. Subsequently (1886), Haswell synonymised the two species as *T. sylvaticus*. Thomson (1893) figured some specimens from near "The Springs", Tasmania, identifying them as *T. sylvaticus*, while noting differences both within the material and between his specimens and Haswell's types. In his discussion of *T. alluaudi* Chevreux from the Seychelles, Chevreux (1901) figured pleopod 1 of *T. sylvaticus* from Australia.

A new species of landhopper was added by Sayce (1909) when he described *T. kershawi* from Victoria. He also redescribed *T. sylvaticus* from Victorian specimens, giving the fullest description of that species so far published. Smith (1909) noted that he found some specimens of *T. sylvaticus* near the Magnet Mine, western Tasmania. Calman (1912) gave some details of the pleopods of specimens of *T. sylvaticus* from Sydney (Port Jackson), whilst Chilton (1916) described a specimen of *T. sylvaticus* from Barrington Tops, distinguishing features of this species, and later (1923) referred to this species some material from Hunter's Hill, Sydney. Hunt, in his review (1925) of the genus *Talitrus*, figured the pleopods of the specimen of *T. sylvaticus* from Australia which were described by Calman (1912) and some details of an undescribed species from Tasmania, which he thought might belong to the genus *Parorchestia* Stebbing.

In his "Crustacea of South Australia" (1929), Hale listed both *T. sylvaticus* and *T. kershawi* as occurring in damp situations near Adelaide. After examining specimens from the Blue Mountains (N.S.W.), Schellenberg

(1934) deduced that *T. dorrieni* Hunt (1925) was native to Australia. Stephensen's review article on indo-pacific terrestrial Talitridae (1935a) listed the terrestrial species previously recorded from Australia. Ruffo (1949a) described a further species, *T. tasmaniae*, from old material in an Italian museum.

In his treatment of *Talitrus*, Hurley (1955) synonymised *T. sylvaticus* and *T. dorrieni*, described the new species *T. pacificus*, recording it from Fingal's Bay, N.S.W., and listed also *T. kershawi* and *T. tasmaniae* as the Australian representatives of the genus. He also included the supralittoral *Orchestia diemenensis* (Haswell) in the Australian landhopper fauna in his review (1959) of the world literature on terrestrial amphipods. In a more recent review of *Talitrus* (1975a), Hurley proposed new subgeneric divisions, but described no new material.

Finally, Bousfield (1976) described *Parorchestia gowerensis* from Lord Howe I., and two further new species, *T. vulgaris* and *T. angulosus* were recently described from Tasmania by Friend (1979).

Non-taxonomic publications on terrestrial amphipods

Most of the literature on terrestrial amphipods deals with their taxonomy and contains little natural history, as the taxonomists were rarely the collectors. However, a small number of articles exists which contains the bulk of published knowledge of the biology and ecology of the group, and these are summarised below (species names as used by authors).

The earliest of these articles was by Grimmett (1926) who, in a general study of the leaf-litter habitat, presented amphipod densities and found sex ratios heavily biased towards females, in a New Zealand forest. Observations on the population structure and body pigments of the introduced *Talitroides dorrieni* (Hunt) were later published by Rawlinson (1937) in an article recording this species from beside Kylemore Lough, in Ireland. Terrestrial amphipods occur in the forest to the south and west of the great escarpment in South Africa (Lawrence 1952) and notes on many aspects of the life of the South African species *Talitroides eastwoodae* (Methuen) appeared

in Lawrence's work (1953) on the biology of the cryptic fauna of forests.

Mallis (1942) reported that great numbers of the introduced *Talitrus sylvaticus* Haswell periodically invaded houses in California, quickly dying due to the lack of moisture. This species was later listed as a pest (Mallis, 1953) but no control measures were recommended.

In a remarkably early, though largely unrecognized study of population energetics, Clark (Ph.D. thesis, 1954) formulated a budget for *Talitrus sylvaticus* in subtropical rainforest near Wollongong, N.S.W. He measured consumption and egestion rates of animals in the laboratory, using these results together with estimates of population density to calculate population consumption, egestion and assimilation rates. Oxygen consumption measurements were used to compute the "annual energy utilization" of the population. Comparing these parameters with an estimate of annual litter fall at his study site, Clark calculated that the *Talitrus* population consumed 24%, digested 5% and converted to heat 1.3% of the annual litter fall in the forest. Unfortunately, only the results of his respirometry were published (Clark, 1955); these demonstrated that the oxygen consumption of *T. sylvaticus* at certain temperatures was higher in winter than in summer.

In a general article on terrestrial amphipods, Hurley (1959) provided a large amount of new information and reviewed the existing literature, making a number of observations on the special adaptations of the group, and its world distribution. This paper was later brought up to date (Hurley, 1968); new information was added, and the author further developed his ideas about the evolution and zoogeography of landhoppers (Section 4.1). Bousfield (1968) added his comments to this zoogeographical discussion, supporting continental drift as an explanation for the distribution of some groups.

The first published autecological work on terrestrial amphipods was provided by Duncan (1969) who studied the ecology of two local species, *Orchestia hurleyi* Duncan and *O. patersoni* (Stephensen) in waste grassland in Dunedin, New Zealand. He provided population data for these species over one year, finding a winter hiatus in breeding. Amphipod biomass reached a

maximum of over 20 g/m^2 in summer, and total amphipod numbers varied with litter thickness at the point sampled. Although *O. patersoni* was found to be more reproductively efficient, *O. hurleyi* has adapted to climbing grass stems, thus utilizing a more extensive microhabitat.

Quantitative ecological information on the land amphipods of Japan is to be found in Saito and Kudara's article (1972) on reproduction of a population of *Orchestia platensis* Krøyer in a forest in Chiba Prefecture, near Tokyo. Another Japanese study, on *O. platensis japonica* (Tattersall) in cedar forest near Mito, was published by Tamura and Koseki (1974). Two sub-populations were found here, apparently maturing and breeding at different times, with a resultant tendency towards genetic separation.

A scanning electron microscope study by Dahl (1973) on supralittoral and terrestrial talitrids revealed two basic types of spines arming the appendages of animals from both habitat types, for which a chemosensory function was proposed.

Two articles on the introduced *Talitroides dorrieni* (Hunt) (Murphy, 1973, 1974) in the British Isles provided a review of that species and showed that it is apparently increasing its range in S.W. England. A more detailed investigation of this species in areas of Cornwall and the Isles of Scilly (Richardson, in press) supplied quantitative data on population density and structure while allowing speculation on factors limiting this invasion.

The description of the troglodytic *Spelaeorchestia koloana* Bousfield and Howarth (1976) from Kauai (Hawaiian Islands) was accompanied by detailed notes on its habitat, biology and zoogeography. Much of this biological information applies generally to land amphipods, but had not been recorded previously.

In a study of two closely related coexisting Tasmanian species, Friend and Richardson (1977) found a vertical separation of microhabitat, and suggested that space is the resource controlling population numbers. Australian landhoppers again received attention in Sandell's (1977) article

on their occurrence in Victoria where, of seven species found, only *Talitrus kershawi* Sayce and *T. sylvaticus* Haswell have been described.

Wildish (1979) found a gradation of reproductive and growth parameters in three British littoral *Orchestia* species occupying successively higher shore habitats. He found also that this gradation approached the situation apparent in primitive terrestrial species from Hurley's study (1957) of some New Zealand landhoppers.

There are many articles on forest ecology in which terrestrial amphipods are mentioned as part of the litter fauna. Australian examples include: Searle (1927) on the food of lyre-birds; Campbell and Gray (1942) who counted the density of amphipods in a lyre-bird habitat; Birch and Clark (1953) who applied Lindeman's (1942) trophic-dynamic approach to the study of forest ecosystems; Howard (1975) on litter fauna of *Nothofagus* forests; Ashton (1975) on litter decomposition in *Eucalyptus regnans* forests; Springett (1976) writing on the effect of prescribed burning on the litter fauna in Western Australian forests.

Present knowledge of the biology of terrestrial amphipods is thus scattered over a wide range of habitat types and species. It is hoped that the present study will allow a greater understanding of the group in south-eastern Australia.

PART I

TAXONOMY AND

ZOOGEOGRAPHY

CHAPTER TWO

APPROACH TO SYSTEMATICS

Introduction

Despite the quantity of published discussion about the generic division of the terrestrial talitrid amphipods (reviewed below), no proposed scheme has been universally accepted. All schemes, however, have been based historically on the system developed in the nineteenth century (Nicolet, 1849; Dana, 1850, 1852, 1853 and 1855; Bate, 1857, 1862; Stebbing, 1888), using sexual differences in gnathopod form to separate the supralittoral amphipods into the genera *Orchestia* Leach, *Talitrus* Latreille, *Talorchestia* Dana and *Orchestoidea* Nicolet. Landhopper species have since been described which, using this system, are placed in the first three genera. The different facies and other distinctive features of many of these amphipods relative to the beach-hoppers have stimulated a number of attempts to separate the various groups generically. The history of this process is reviewed in this chapter, and some recommendations are made for future work.

Review of terrestrial amphipod systematics

Before 1898, all described terrestrial amphipod species were assigned either to *Orchestia* Leach, if there was sexual dimorphism in the gnathopod form, or to *Talitrus* Latreille if this was absent.

Bonnier (*in* Willem, 1898) proposed the generic name *Talitroides* for an amphipod which was found in a glasshouse in Belgium, without giving it a specific name. This genus was distinguished from *Talitrus* mainly the possession of reduced pleopods. The species was named *Talitroides bonnieri* by Stebbing (1906), but was later found to be synonymous with *Talitrus alluaudi* Chevreux (Calman, 1912; Chevreux, 1913; Stephensen, 1925; Schellenberg, 1934), which therefore became the type species of the genus *Talitroides*.

In 1899, the genus *Parorchestia* was created by Stebbing to receive the *Orchestia tenuis* Dana, *O. hawaiiensis* Dana and *O. sylvicola* Dana, which were all thought to occur in terrestrial situations (Stebbing, 1906). These species were distinguished from other members of *Orchestia* by the possession of a distinct fourth segment on the palp of the maxilliped. Thus the terrestrial amphipods were grouped in four genera, all of which belonged to the family Orchestidae Leach 1813-1814. This name was changed to Talitridae by Stebbing (1900) who, in his revision of the world Gammaridea (1906), recognized thirteen genera comprising the family: *Talitrus*, *Talitroides*, *Orchestoidea*, *Orchestia*, *Talorchestia*, *Ceina*, *Chiltonia*, *Parhyale*, *Neobule*, *Parorchestia*, *Hyale*, *Hyalella* and *Allorchestes*. The family grouping remained stable for over fifty years; however, among the terrestrial species, generic divisions were frequently changed and disputed.

The sexually similar group

Landhoppers can be broadly divided into the species showing sexual dimorphism of the gnathopods (the sexually dimorphic group) and those lacking this dimorphism (the sexually similar group). The history of the classification of the latter group of species is rather involved and has resulted in confusion, for a number of reasons. Principal amongst these is the heavy reliance of early amphipod taxonomists on the form of the gnathopods in generic classification. The reluctance of many later workers to place similar weight on other characters is demonstrated by their failure to remove terrestrial species from their original classification with another sexually similar talitrid, *Talitrus saltator* Montagu. This is despite the distinct heavy-bodied, spinous facies and obviously different ecology and distribution of this European sandhopper. The fact that most of the taxonomists involved were working in Europe and had little or no experience of living landhoppers must have had substantial bearing on their thinking.

In 1913, Methuen erected another genus, *Talitriator*, to receive

the new species *T. eastwoodae* Methuen from South Africa, differing from *Talitrus* in the shape of the coxa of pereopod 5 and several other characters, including the possession of a fourth segment on the maxilliped palp. K.H. Barnard (1916) united the Australian species *T. sylvaticus* and *T. kershawi* in *Talitriator* with *T. eastwoodae*, while Stebbing (1917) also recognized this genus, but synonymised Methuen's species with Spence Bate's (1862) *Talitrus africanus*. Hunt (1925), however, found fault with all the characters separating *Talitriator* from *Talitrus*. Schellenberg (1934) saw no difference between *Talitriator* and *Talitroides*, but preferred to retain the distinction between the supralittoral *Talitrus* and the "genetischen Einheit" of the terrestrial species grouped as *Talitroides*. Burt (1934) did not recognize *Talitroides*, but set up a new subgenus *Talitrus (Talitropsis)* for his new species *T. (T.) topitotum* because it apparently lacked a palp on maxilla 1.

During the next twenty years or so, however, the most common practice was to retain the genus *Talitroides* for the terrestrial representatives. K.H. Barnard (1936) pointed out that splitting *Talitroides* from *Talitrus* on the basis of pleopod reduction would necessitate similar splits in *Talorchestia* and *Parorchestia*, but he later (1940) demonstrated that two other characters separate *Talitrus saltator* from the terrestrial species (grouped as *Talitroides*). These are the distinctive broad spinose maxilliped palp and subcircular segment 2 of pereopod 5 of the supralittoral species. In 1958 he also included Burt's subgenus *Talitrus (Talitropsis)* with *Talitroides*.

Although Stephensen (1925) had synonymised *Talitroides* with *Talitrus*, in his later paper on a Melanesian species (1943) he held them separate because of the reduction of pleopod 3 in the terrestrial species. Reid (1947) emphasised different characters, combining the "non-toothed antennae", lateral compression and pleopod degradation found in the landhoppers to exclude *T. saltator*.

A sub-generic division between *Talitrus* and *Talitroides* was preferred by Ruffo (1949a, 1949b, 1958) after he found specimens of *T. gulliveri* from Annobon I. in the Gulf of Guinea to be intermediate in the form of maxilliped and pleopods between the two types. Hurley (1955) also recommended this course of action. In a world revision of the talitrid amphipods, Bulycheva (1957) synonymised *Talitroides* and *Talitriator* with *Talitrus*, while J.L. Barnard (1960) followed suit by placing four new Micronesian landhoppers in *Talitrus*.

A move to retain and strengthen the divisions came from Bousfield (1958) who maintained that *Talitrus* and *Talitroides* are distantly related genera, sharing only the mitten-shaped male second gnathopod. He placed *Talitrus pacificus* Hurley in *Talitroides* (1961) and later (Bousfield and Carlton 1967) expressed the opinion that *Talitrus sylvaticus* belongs to a separate Australian genus with three other species. A further development, due to Bousfield (1971), was the description of a new genus, *Brevitalitrus*, represented by a number of Micronesian and Melanesian species, while he recognized the existence of *Talitroides* and *Talitriator*. Most recently, Hurley (1975a) relaxed his stance by proposing further division of the sexually similar species into eight subgenera, adding *Arcitalitrus*, *Keratroides* and *Mysticotalitrus* to the previously-used taxa *Talitrus*, *Talitriator*, *Talitroides*, *Talitropsis* and *Brevitalitrus*.

In conclusion, it must be stated that despite the diversity of opinion on generic divisions, the taxonomy of the sexually similar group shows a fairly high degree of organization. While the taxonomic system which emerges from the present study (Chapter 3) agrees in a number of points with that of D.E. Hurley (1975a), the innovative approach of E.L. Bousfield (e.g. 1964, 1971, 1978) has given much inspiration to the present author.

Terrestrial species allocated to *Talorchestia* Dana

Seven landhopper species have been assigned at one time or another, to the genus *Talorchestia*. The authors involved (see Table 2.1) have placed their species on the basis of the form of the female first gnathopod (in conjunction with the form of the other gnathopods), which is subchelate in *Orchestia* and simple in *Talorchestia*. Where the gnathopod is slender (as is often the case with terrestrial species) the difference between these forms is slight. Indeed, Vader (1970) has demonstrated difficulties with the reliance upon gnathopod form for diagnosis even of sandhoppers, and has recommended the development of different characters. The assignment of these terrestrial species has generally been questioned by later authors, where subsequent treatments exist, as shown in Table 2.1. It is significant that only three workers have placed terrestrial species in *Talorchestia* while a far greater number have assigned these species differently.

The genus *Talorchestia* is composed of species inhabiting the supralittoral zone, generally with a preference for sandy beaches (Morino, 1972). The members of the genus, more so than the supralittoral *Orchestia* species, exhibit a homogeneous facies, heavy-bodied and spinous, with stout appendages, suited for burrowing in sand (Bousfield, 1973). As discussed below (Section 3.3) the sand-burrowing habit is a morphological and behavioural specialization of the beach-drift-cryptozoic habit for which the sublittoral and littoral Hyalidae, and presumably the primitive talitroidean, were pre-adapted. The genus *Orchestia* is much larger than any of the other three supralittoral talitrid genera and more diverse than them both in morphology and in ecology. It is by far the most likely to have formed the stock from which invading species arose, and moved from beach-drift to forest litter.

Where adequately described, the species listed in Table 2.1 prove to be slender animals, lacking the spinosity of appendages (especially the

TABLE 2.1 Treatment of terrestrial amphipod species assigned at some time to *Talorchestia* Dana.

Original description	Placement in <i>Talorchestia</i>	Subsequent treatment
		Two species (<i>Orchestia</i> sp. and <i>Talitrus</i> sp.) (Ruffo and Paiotta, 1972)
<i>Talorchestia antennulata</i> Chevreux, 1915	Chevreux, 1915	
<i>Talorchestia japonica</i> Tattersall, 1922	Tattersall, 1922	= <i>Orchestia platensis japonica</i> (Iwasa, 1939)
<i>Talorchestia kempfi</i> Tattersall, 1914	Tattersall, 1914	
<i>Talorchestia malayensis</i> Tattersall, 1922	Tattersall, 1922	= <i>Orchestia anomala</i> Chevreux (Schellenberg, 1938; Bousfield, 1971)
<i>Orchestia parvispinosa</i> Weber, 1892	Tattersall, 1914	
<i>Talorchestia patersoni</i> Stephensen, 1938	Stephensen, 1938	<i>Orchestia patersoni</i> (Hurley, 1957)
<i>Orchestia rectimana</i> Dana, 1852	Chevreux, 1907	<i>Talorchestia rectimana</i> (Stephensen, 1935b)

maxillipeds, uropods and telson) typical of *Talorchestia* sandhoppers. There is also an Australian landhopper, occurring in southern Victoria and on King I., which would be classified, on gnathopod form only, as *Talorchestia*. However, its slender body, long appendages, vestigial pleopods and modified gills make this obviously incorrect, and the creation of a new genus is desirable.

The indications are, then, that these land amphipods (Table 2.1) have been wrongly grouped as *Talorchestia*, being similar to other species of that genus only in gnathopod configuration. Without examining material it is difficult to propose generic relationships, but it is most likely that these species have arisen, independently of *Talorchestia*, from *Orchestia* stock. Perhaps the most important indication is that too much weight has been placed on gnathopod form in talitrid taxonomy. This subject will be discussed further in Chapter 3.

History of the genus *Parorchestia* Stebbing

The genus *Parorchestia* was created by Stebbing (1899) who separated *Orchestia tenuis*, *O. hawaiiensis* and *O. sylvicola* from other known species of *Orchestia* by the possession of a small but distinct conical fourth segment on the maxilliped palp, which carries a spine on its truncate apex. The distinctiveness of this character is doubtful, and it may be that Stebbing found that it was correlated in these species with a combination of more obvious characters. In "Fauna Hawaiiensis" (1900) he listed features of *P. hawaiiensis* which separated this species from *Orchestia pickeringii* and *O. platensis* from the Hawaiian Islands, some of which are thought (Chilton, 1909a, 1912; Bousfield, 1964) to indicate greater specialization for terrestrial life (long antennae, slender poorly spined maxilliped palp, development of gnathopod lobes).

Chilton (1909a) recognized that although *Orchestia* species sometimes have an obscure fourth segment on the maxilliped, it is convenient to group the terrestrial species (as *Parorchestia*) as these are also distinguished by long slender spines on the antennae and pereopods, and the

possession of more reduced pleopods. He added *P. improvisa*, *P. insularis*, *P. maynei* and *P. parva* to the genus from terrestrial situations in the subantarctic islands of New Zealand.

Chevreaux (1915) cast doubt on previous work by stating that of the seven previously described species, four were perhaps not of this genus. He described two new species, *P. sarasini* (terrestrial) and *P. pusilla* (found in freshwater habitats) from New Caledonia.

Two species from Luzon, *P. luzonensis* (terrestrial) and *P. lagunae* (freshwater littoral) were added to the genus by Baker (1915), while from South African coastal specimens, Barnard (1916) described a new species, *P. dassenensis* and identified others as *P. tenuis*. Shoemaker (1935) listed all twelve of these species and added a new terrestrial species from North Borneo, *P. kinabaluensis*.

From material in the Indian Museum, Barnard (1935) described *P. notabilis* from Cochin State. In 1940, he reallocated material formerly identified as *P. tenuis* by himself (1916) and Stebbing (1922) to *P. rectipalma* n.sp. and *P. dassenensis* Barnard (1916), respectively.

In an article on some crustaceans from the subantarctic, Stephensen (1938) drew attention to the spination of the uropods of *Parorchestia* species. He noted the tendency of the females to have the outer ramus of uropod 1 naked, and the outer ramus of uropod 2 bearing marginal spines. Previously, in a review (1935a) he had listed the spination of uropod 1 for species of *Orchestia* and *Parorchestia* from the Indo-pacific region. Although in his earlier paper, Stephensen made no comment about the consistency of this character, we may continue this analysis from the data he provided. If the nakedness of uropod 1 outer ramus were to be diagnostic of *Parorchestia*, of the species Stephensen lists, 10 out of 25 *Orchestia* species and varieties, and 3 out of 11 *Parorchestia* species would have to be transferred to the other genus. Reorganization on this scale would have to be justified with reference to further characters. It is interesting to note, however, that

the majority of supralittoral species listed by Stephensen (1935a) have the outer ramus of uropod 1 with marginal spines (10 out of 12) and most terrestrial species listed have this ramus marginally naked (11 out of 17). Seven further species in Stephensen's list cannot be easily categorised, through lack of information.

A possible solution to the problem of generic division was advanced by Shoemaker (1942) who, while quoting Chilton's remarks (1909a) about the terrestrial facies, regarded *Orchestia* and *Parorchestia* as synonyms because in his opinion, the distinguishing characters differ only in degree. He was followed by Ruffo (1949a), who allocated *P. kinabaluensis* to *Orchestia* when he found specimens possibly referable to it amongst material from New Guinea.

A rather more thorough review was provided by Hurley (1957) in his treatment of the New Zealand supralittoral and terrestrial species. He recounted the development of the definition of *Parorchestia* as intermediate forms were discovered, and pointed out the difficulties of using either the form of maxilliped palp segment 4 or ecological criteria to separate the genera. Stephensen's uropod spination character would involve unprofitable reorganization, in Hurley's opinion, and the use of pleopod reduction, found in many *Parorchestia* species, was ruled out as it also occurs within the genus *Talitrus* (*sensu lato*). In agreement with Shoemaker and Ruffo, he synonymised the genera *Orchestia* and *Parorchestia*, retaining only a subgeneric distinction between the supralittoral [as *O. (Orchestia)*] and terrestrial [*O. (Parorchestia)*] species.

In her world revision, Bulycheva (1957) adopted the form of gnathopods for generic classification in the family Talitridae (*sensu stricto*); thus *Orchestia* and *Parorchestia* were synonymised, without discussion. Another point of view, however, was offered by Bousfield (1964) who maintained the separate identity of *Parorchestia* (as in Bousfield, 1961) and suggested that the genus be restricted to species resembling *P. tenuis*

(as described by Stebbing, 1906), with short, sparsely setose antennae, short stout peraeopods, short thick dactyls, long pleopods, sac-like gills and broad brood-plates. In his opinion, further genera should be created for species conforming to the typical landhopper facies, with long slender appendages, reduced pleopods, highly modified gills and narrow oöstegites. This opinion was later reiterated (Bousfield 1971), with the descriptions of two new species, *P. macrochela* and *P. similis* from Luf I., Bismarck Archipelago.

Barnard (1969) and Ruffo and Paiotta (1972) used the broad definition of *Orchestia* while Bousfield (1976) continued to foreshadow further division of the group, while describing *P. gowerensis* from Lord Howe I., a species apparently falling between the two groups he referred to previously (1964).

At present, therefore, there is a diversity of opinion on the reality of the *Parorchestia* concept, mainly polarised into two schools, one denying its existence and the other seeing it as one of a number of groups of sexually dimorphic landhopper species.

The group *Orchestia sensu lato* (i.e. including *Parorchestia*) is undeniably large, comprising over 100 species (Bousfield, 1976) and distinct morphological groups exist within it (see Section 3.3). Hurley (1968) and Bousfield (1968) agree in proposing that sexually dimorphic landhoppers have most probably arisen a number of times in different localities from supralittoral *Orchestia* species. A single grouping of these landhoppers is thus in danger of being polyphyletic. To attempt a true representation of the phylogenetic history of the group, then, two possibilities are open. The first is to include all sexually dimorphic species with the supralittoral groups which apparently gave rise to them, possibly as *Orchestia*, as proposed by Hurley (1957). The second possibility, which is preferable for the reasons given above, but more difficult, is to form genera of sexually dimorphic species so that for each genus, morphological and, less importantly,

zoogeographic evidence is consistent with an origin in a single invasion.

The present problem, however, is to establish the identity of *Parorchestia*, so that assignment of sexually dimorphic terrestrial species may be facilitated. In his original diagnosis of the genus, Stebbing (1899) merely listed the three constituent species, *P. tenuis*, *P. hawaiiensis* and *P. sylvicola*, without naming a type species. Bousfield (1964), has stated that morphologically divergent groups exist within Stebbing's concept of *Parorchestia*, and has suggested that the name be applied to the group with the closest affinity to *P. tenuis*. The identity of this species, and that of *P. sylvicola*, is in some doubt, and some investigation is necessary. These species are discussed further, below. *P. hawaiiensis*, however, has been recently identified amongst endemic species from the Hawaiian chain (E.L. Bousfield, pers. comm.).

Parorchestia tenuis (Dana, 1852)

The "scientific gentlemen" of the U.S. Exploring Expedition (Wilkes, 1845) including J.D. Dana, were based at Bay of Islands, North Island of New Zealand, from 24 March until 6 April 1840. Amongst the collections resulting from this visit was a female amphipod which Dana later (1852, 1853 and 1855) described with figures, as *Orchestia tenuis*, so named, presumably, because of its "very slender" flagellum of antenna 2. The locality was given as "Bay of Islands" with no habitat details. The information contained in this work was not added to by any reviewing author (Bate, 1862; Miers, 1876; Thomson, 1881; Thomson and Chilton, 1886; della Valle, 1893; Thomson, 1898) until, in setting up the genus *Parorchestia*, Stebbing (1899) recorded that in *P. tenuis* (as in two other species) "the maxillipeds have a fourth joint to the palp, distinct, though small, conical, and carrying a spine on the truncate apex." Presumably, Stebbing was working on the same material when he later redescribed *P. tenuis* (1906); this was apparently not Dana's material, as it included a male, and Stebbing

draws attention to differences from Dana's description. Stebbing's specimens appear to have been terrestrial, as he gives the habitat of *P. tenuis* as "New Zealand. Among roots and grasses....". The other habitat given "...and in a small stream" refers to Thomson's *Allorchestes recens* (1884) which Stebbing (1899) wrongly (see below) synonymised with *P. tenuis*.

This new description disagrees with the original in very few points, mainly because Dana's text contains few points by which a species of *Orchestia sensu lato* may be distinguished. The most important difference concerns the 2nd antennae, which in Dana's specimen are long (half as long as the body) and possess fourteen flagellar segments. Stebbing's specimens have shorter antennae (less than half body length); he gives a range of eight to fourteen flagellar segments. This rather large range may indicate sexual dimorphism (not described) or the presence of juveniles in Stebbing's material; however it is more probable that the range was extended to include Dana's specimen. From Dana's diagram, his specimen apparently possesses two or three segments more than Stebbing's in the flagellum of the first antenna.

This evidence for questioning Stebbing's allocation of his specimens to *P. tenuis* is, admittedly, slim; the two descriptions contain only a scattering of points on which direct comparison can be made, and Stebbing provides no figure. However, simply acknowledging the probable richness of the New Zealand land amphipod fauna (Bousfield, 1964), one sees that the likelihood of these being separate species is quite high.

Later identifications of *P. tenuis* were based on Stebbing's redescription. Describing the freshwater amphipods of New Zealand, Chilton (1909b) identified several specimens from "a freshwater stream at Rona Bay," Wellington Harbour, as *P. tenuis* Stebbing, suggesting that the species may be found in brackish, freshwater or terrestrial situations. I have examined a male and a female specimen, marked "Rona Bay (freshwater stream),

Wellington Harbour, 1905" from the Chilton Collection, Canterbury Museum, and found them to agree completely with Thomson's description (1884) of *Allorchestes recens* (which is obviously an *Orchestia*, as pointed out by Hurley, 1975b). They differ from *P. tenuis* (Dana) in their very short antenna 2 and smaller size, and from *P. tenuis* Stebbing in the equal segments 2 and 3 of antenna 1, pleopod rami which are longer than the peduncles, slightly cleft telson and smaller size. Also referable to this species is a female, marked Rona Bay, 1923, from this collection. Chilton (1909a) ascribed a few small specimens from a similar habitat at Perseverance Harbour, Campbell I., to *P. tenuis* Stebbing, after comparing them with New Zealand specimens.

Two male amphipods in the Chilton collection labelled *P. tenuis* were collected in the Kermadec Is., one being marked "freshwater". These are apparently part of the material referred to by Chilton (1911) from a freshwater stream on Sunday Island. They differ on a number of points from *P. tenuis* (Dana), *P. tenuis* Stebbing and *O. recens* (Thomson) perhaps most significantly, in having the outer rami of uropods 1 and 2 armed with several marginal spines. Another male of the same species is present in the collection, marked "Portage, Kenepuru Sound", which is in the north of the South Island, New Zealand. A female specimen from brackish water in Torea Bay, Queen Charlotte Sound, referable to yet another species of *Orchestia* s.l. has been identified by Chilton as "*P. tenuis*"; the very long pleopod rami and short seventh peraeopods separate it from the other species.

Finally, *P. tenuis* has also been recorded from "Wet cliffs, Manukau" (Chatham Is: Chilton 1925). Thus besides Barnard's (1916) and Stebbing's (1922) mistaken identification of some South African material (mentioned earlier) there are no further records of the species before Hurley's review of *Orchestia* s.l. (1957) and treatment of the New Zealand species.

As stated earlier, Hurley (1957) synonymised *Orchestia* and *Parorchestia* because of the inconsistency of the characters being used to

separate them. In dealing with *O. tenuis*, he compared Dana's descriptions (1852; 1853 and 1855) of this species and *O. sylvicola* and decided that Dana's male (which Dana assigned with reservations, to *O. sylvicola*) belonged to *O. tenuis*. He could not find significant differences between Stebbing's redescrptions (1906) of the two species, and regarded *O. sylvicola* as a *nomen dubium*. Hurley also described a landhopper species, apparently common in New Zealand, as *O. tenuis*. This species differs in a number of significant points, from both Dana's and Stebbing's descriptions of *O. tenuis*. As described by Hurley, *O. tenuis* has long second antennae, which, although his male specimen was smaller than Dana's female, has 22 flagellar segments as compared with 14, and his female has 30. Hurley's specimen's first antennal flagellum is equal to the peduncle whereas that of Dana's is longer, and the sixth peraeopod, shorter than the seventh in *O. tenuis* Dana, is "much the longest".

Hurley's species differs from *P. tenuis* Stebbing in the greater number of second antennal flagellum segments, in telson spination and in the second segment of the first antenna being shorter than the third in contrast to that of Stebbing's species. Perhaps the most significant difference concerns the coxal gills, which in *P. tenuis* Stebbing are oval, whereas Hurley's diagrams show a large well-developed lobate gill of the second gnathopod and the fifth and sixth peraeopod gills small but modified.

It must therefore be concluded that no subsequent worker has dealt with *P. tenuis* (Dana), and research on topotype material from Bay of Islands is necessary before this species can be identified. Dana's description of *P. tenuis* lacks sufficient detail to enable a precise definition of its generic group.

Parorchestia sylvicola (Dana, 1852)

It is clear that the female on which Dana based the description of *Orchestia sylvicola* (1852, 1853 and 1855) was terrestrial, as it was amongst a collection taken, during the stay at Bay of Islands, "from moist

soil in the bottom of the extinct volcano of Taiamai, twenty miles from the sea, and about the joints of succulent plants". Dana's work contains the first records of amphipods in terrestrial situations, well away from the sea. His description of this species was not very detailed, but he did list two rather distinctive features. These were firstly, that the first uropod outer ramus bore marginal spines, and secondly, that the fifth peduncular segment of the second antenna was only two-thirds the length of the fourth segment. This latter feature is very unusual in land amphipods (segment 5 is typically longer than segment 4) and may be due to a mistake in description (Dana's drawing appears to show subequal fourth and fifth segments). If the text represents the true situation, however, then no subsequent worker has dealt with *O. sylvicola*.

Bate (1862) provided a short description of a male amphipod from New Zealand, apparently found in a terrestrial habitat, which he identified as *O. sylvicola*. Apart from the form of the second antenna, this description differs very little, in characters not displaying sexual dimorphism, from Dana's description of the female from Taiamai. Bate's drawings, like Dana's, are not very informative.

After placing this species in his new genus *Parorchestia* (1899), Stebbing (1906) redescribed *P. tenuis* more fully than did either Dana or Bate, but provided no illustrations. Stebbing's specimens differed from Dana's in both the form of the second antenna (as mentioned above) and in the fact that the first uropod outer ramal margins were naked, in both sexes.

The only other description of new material which might throw some light on the identity of *P. sylvicola* is that of *O. tenuis* by Hurley (1957). It has already been suggested that this author was not dealing with *O. tenuis* Dana. As this description gives the uropod 1 outer ramus as naked (in both sexes), it seems that Hurley had specimens of yet another species. Hurley's description of *O. tenuis* differs from Stebbing's description of *P. sylvicola* in the relative lengths of pereopods 6 and 7.

The morphology of *P. sylvicola* is therefore known only from the limited information contained in Dana's original work. The type specimens are apparently lost (Hurley, 1957). Once again, topotype material must become available before this problem can be solved.

Conclusions

It appears that *P. hawaiiensis* is the only one of Stebbing's original *Parorchestia* species about which detailed morphological information might be available. It is suggested that, if the name is to be retained, it should be applied to *P. hawaiiensis* and closely related species. This is preferable to the retention of the heterogeneous, possibly polyphyletic assemblage of forms to which this generic name has been attached.

The descriptions and illustrations of both Dana (1853 and 1855) and Stebbing (1900) of *P. hawaiiensis* refer to a slender animal with long appendages, displaying a number of apomorphic features (Chapter 3), while retaining sexually dimorphic gnathopods. There is only one Tasmanian species (*Neorchestia plicibrancha* sp.n. - see Chapter 3) in which this facies exists. There are, however, broad areas of difference (in the form of maxillipeds, gnathopods, uropods and telson) which remove the likelihood of any close relationship between these two species.

The genus *Parorchestia* will not, therefore, be employed in the taxonomic section of the present study. It is evident that further information on the land amphipods of New Zealand and the Hawaiian Islands must become available before the status of this taxon can be established.

CHAPTER THREE

TAXONOMY

Section 3.1 Introduction

Taxonomic publications on the land amphipods of Tasmania are restricted to six articles (see Chapter 1). Only three species described or recorded from Tasmania in these works definitely occur there. During this study, collections were made not only on the island itself, but also on its offshore islands, islands in Bass Strait, and on the mainland of Australia. Many undescribed species were found, but it was necessary to restrict this taxonomic study to embrace only the species found on the Tasmanian mainland. Examination of other specimens has enabled wider taxonomic and zoogeographic conclusions to be drawn, but this material will not be treated formally here. The single species which has been found on both sides of Bass Strait is not described fully below, but left for treatment in other work now in progress.

The name "Tasmania" as used here, refers to the geographical area within the State boundaries, but excluding Macquarie Island. In addition to the main island then, all offshore islands, and the islands in Bass Strait as far north as the Hogan Group are included. The large land mass is designated "the Tasmanian mainland".

Section 3.2 Methods

Collection and Preservation

Landhoppers are very easily damaged, but are also prone to jump violently in their efforts to escape. The use of forceps in collection is therefore not recommended, as rather more gentle methods are needed. The most successful rapid method involves sucking the animals directly off the ground or from soil and litter on a drop-sheet,

using an aspirator. This is simply constructed from a large screw-top or corked vial, plastic tubing and fine-meshed gauze.

More efficient but slower extraction is carried out by taking samples of soil and leaf litter from the field in calico bags (cloth minimises drowning in condensed water) and extracting the amphipods either manually or by heat extraction in modified Tullgren apparatus.

The animals are preserved in 70% ethanol with 2% glycerol added to keep joints flexible and to guard against damage from evaporation of the alcohol mixture.

Study, Dissection and Drawing

Specimens were inspected under 70% ethanol using a stereo-microscope. It was one of the aims of the study to produce a system of identifying landhoppers at this level of examination, without dissection. For the taxonomic study reported in this chapter, dissection was necessary, and was carried out after the methods laid out by Barnard (1969). Watchmakers forceps (Dumont types 3 and 5) were indispensable instruments, as were needles made from Minuten entomological pins mounted in epoxy cement on the blunt ends of fine wooden skewers. A small knife made from a pointed piece of blade from a safety razor mounted in a screw-clamp handle facilitated the removal of epimeral plates and telsons, although a Zeigler eye-surgeon's knife later proved ideal for this purpose. Making temporary mounts of appendages in glycerol allowed these to be turned over if need be, during the drawing process. Cavity slides were employed to mount uropods 1 and 2, to provide a lateral view. To prevent the collapse of some delicate structures (especially the tumid lobes on some gnathopods) due to osmotic differences, the appendages were transferred from 70% ethanol + glycerol to open crystal dishes containing a 17:3 mixture of absolute ethanol and glycerol, and the ethanol allowed to evaporate slowly. In making permanent slides,

Canada balsam was used to mount parts of type specimens.

All appendages and mouthparts were drawn from the preparations mentioned above. Several methods were used. A Zeiss camera lucida mounted on an Olympus EH compound microscope with a vertical camera tube was used for early drawings. However, a Leitz Prado microprojector attachment on a Leitz Pradovit 250 slide projector proved the most satisfactory arrangement, using four objectives and three eyepieces to produce a wide range of magnifications. The image was projected onto a mirror held at 45° to the vertical to reflect it down onto the bench to the most convenient drawing position. The drawings of some appendages were subsequently reversed during tracing to represent the correct orientation.

Drawings of whole animals were composed from drawings of individual appendages and of bodies traced from colour transparencies. Photographs in lateral view were taken of all holotypes by Mr. D. Peacock, University of Tasmania.

Section 3.3 Systematics

Superfamily TALITROIDEA Bulychева 1957, revised Bousfield 1978.

Family TALITRIDAE Bulychева 1957.

The present state of systematics of the terrestrial Talitridae and its historical development have been reviewed in Chapter 2. It is suggested that a realistic treatment of the group has not yet appeared and that this is due to the approach used in most previous taxonomic studies.

In the terrestrial Amphipoda, the gammaridean genotype has encountered the harsh environment of the land. These exacting conditions have produced a high degree of uniformity in certain aspects of morphology which has led to the taxonomic "lumping" of a fauna which is, in reality, diverse. It is only when new characters are examined that the true diversity becomes apparent.

The morphology of mouthparts and peraeopods has become important in distinguishing genera of marine amphipods. Those species are free to exploit the many different energy sources and to occupy the many different microhabitats which occur in the sea. On land, however, the limitations of low water availability and high transpiration rate ensure that land amphipods are kept within a much narrower range of microenvironments. The food sources available to them are therefore limited, so there are few selective forces giving rise to radical changes in mouthpart morphology. Movement within the leaf litter/soil substrate calls for a certain peraeopod configuration; that found in the supralittoral talitrids proves satisfactory in the forest floor environment, and has undergone little change there. Amphipods of other families living in marine environments use their peraeopods for many functions besides walking, for example, tube-building, swimming and clinging to current-swept algal fronds. While some terrestrial amphipods have moved into habitats other than the forest floor, like grassland (Duncan, 1969), caves (Bousfield and Howarth, 1976) and leaf-axils of rainforest plants (E.L. Bousfield, pers. comm.) the structure of these new microenvironments is not sufficiently different from forest floor to cause more than lengthening or strengthening of the basic talitrid peraeopod.

On the other hand, the morphology of gills, oostegites and pleopods, which has been used rarely in marine amphipod taxonomy, shows a great diversity amongst landhoppers because of differing degrees of adaptation to terrestrial life. It may be expected that adaptive pressures connected with water retention are among the strongest operating on land amphipods. Many of the extreme morphological changes of the body parts mentioned above may be correlated with the dryness of the habitat or microhabitat in which the animals are found (Chapter 4). Although much of the landhoppers' success must be attributed to physiological and behavioural adaptation (Hurley, 1968), there is a morphological

component which cannot be ignored. This is especially obvious in the Australian fauna, which occurs on a continent where low rainfall environments are widespread, and where the last 60 000 years have seen even drier periods (Bowler *et al.*, 1976).

Not surprisingly, most amphipod taxonomists who have dealt with landhoppers have had their greatest experience with the marine Amphipoda, and have therefore been attuned to the characters which show most variation amongst animals living in the sea. It is suggested that this fact has contributed greatly to the low degree of generic division bestowed upon terrestrial talitrids and that the diversity present has been largely overlooked.

Gnathopod form as a taxonomic character in the Talitridae

The importance of gnathopod form in most taxonomic treatments of landhoppers has been indicated in Chapter 2. The morphological peculiarity of these animals, due to selection in terrestrial environments, has not been fully recognized. Consequently gnathopod form has been given the same weight in terrestrial talitrid taxonomy as in the treatment of marine littoral and supralittoral species, a weight which it does not deserve. To appreciate this, it is necessary to consider gnathopod function in supralittoral and terrestrial species.

A number of observations on gnathopod function in the supralittoral Talitridae may be found in the literature. Recorded uses of male first and second gnathopods (either or both) are in digging (Reid, 1938; Morino, 1972), intraspecific fighting (Smallwood, 1905; Williamson, 1951a) and grasping and carrying the female during amplexus (Smallwood, 1905; Williamson, 1951a; Morino, 1972).

As a general rule, Tasmanian landhoppers do not dig burrows in the soil, although there are some exceptions, mentioned later. Intraspecific fighting is rare: it has been observed, however, between males of a species possessing secondarily enlarged first gnathopods, probably

for this purpose. Full-grown male landhoppers are usually smaller, rarely larger than fully grown females; it appears that the carrying habit is not commonly practised. Obviously, carrying would be much more difficult in leaf litter than on a sandy beach, or in even more physically complex shore environments.

Where gnathopod 1 is subchelate in landhoppers, it tends to be small and fairly weak. There is a tendency, in more advanced species, for this gnathopod to be simple (non-prehensile) (see Table 3.1). A wide range of intermediate stages between these two states may be found, however. Where gnathopod 2 is subchelate, it is generally much smaller than in supralittoral species, although still muscular.

The more consistent adherence to either simple or subchelate forms of the first gnathopod in supralittoral species appears to be related to the functional significance of these forms; in landhoppers, on the other hand, gnathopod shape seems less critical, perhaps because of less specialised use of the appendages.

Taxonomists have tried to force terrestrial species into the supralittoral generic system based on possession of certain combinations of gnathopod shapes in males and females. Amongst land-dwelling species, however, combinations occur other than the four which distinguish the classical genera of beach hoppers, *Orchestia*, *Talorchestia*, *Orchestoidea* and *Talitrus* (Table 3.1.)

Compounding the shortcomings of the classical system is the difficulty in distinguishing between "simple" and "subchelate".

"Simple" means completely lacking a palm, while ideally, a "subchelate" hand has a palm as long as the dactyl, which closes on it; many intermediate forms could exist. The difficulties arising from these definitions have been encountered in supralittoral talitrid taxonomy, usually in assigning species to either *Orchestia* or *Talorchestia* on the basis of the shape of the female's first gnathopod (Shoemaker, 1942; Reid, 1947;

TABLE 3.1

Observed and hypothetical gnathopod combinations in Talitridae

	Gn1 ♂	Gn2 ♂	Gn1 ♀	Gn2 ♀ ¹
<i>Orchestia</i>	subchelate	subchelate	subchelate	mitten-shaped
<i>Talorchestia</i> + landhoppers e.g. undescribed Vic. sp.	subchelate	subchelate	simple	mitten-shaped
<i>Orchestoidea</i>	simple	subchelate	simple	mitten-shaped
<i>Talitrus</i> + landhoppers e.g. <i>Mysticotalitrus crypticus</i>	simple	mitten-shaped	simple	mitten-shaped
<i>Mysticotalitrus tasmaniae</i> + <i>Austrotroides maritimus</i>	subchelate	mitten-shaped	simple	mitten-shaped
<i>Orchestia rubroannulata</i> Hurley + <i>Spelaeorchestia</i> <i>koloana</i> Bousfield	subchelate	mitten-shaped	subchelate	mitten-shaped
As yet undiscovered	simple	subchelate	subchelate	mitten-shaped
	simple	mitten-shaped	subchelate	mitten-shaped

1. The mitten-shaped morphology is the only one which has been observed in the second gnathopod of female talitrids. It is apparently used in the care of the large eggs found in this family.

Vader, 1970; Morino, 1972). It is proposed that other characters should be given precedence over, or at least equal importance with gnathopod form in talitrid taxonomy.

The European sandy beach amphipod *Talitrus saltator* is unique among sandhoppers in its lack of enlarged second gnathopods in the male. A mitten-shaped, minutely chelate hand is found on the second gnathopod, and the first gnathopods are simple. Many landhopper species also display this gnathopod configuration, and on this basis alone, have been placed in the same genus as *Talitrus saltator*, the type species. *T. saltator*, however, more closely resembles a *Talorchestia* in body form and morphology of mouthparts, uropods and telson, and must be seen as a highly specialised sandhopper with complex behavioural adaptations to its habitat (Williamson, 1951b; Pardi and Papi, 1953; Geppetti and Tongiorgi, 1967; Bregazzi and Naylor, 1973; Ercolini and Scapini, 1974; Scapini, 1979). The lack of prehensile gnathopods is compensated for in mating by use of the elongate strong second antennae of the male for grasping the female (Williamson, 1951a); perhaps simple, rather than subchelate gnathopods are more efficient for digging in sand, which this species accomplishes very efficiently (Dahl, 1946). Undue emphasis on gnathopod form as a character has caused the grouping of *T. saltator* with the landhoppers, to which it is only distantly related; it is suggested that the terrestrial species should be separated generically from this sandhopper.

Ruffo (1947a, b) and Hurley (1955, 1957, 1975a) have recognized only two genera containing landhoppers, *Talitrus* and *Orchestia*, which they distinguish on gnathopod configuration. The poor definition of generic boundaries based on this character have been pointed out, as has the existence of further combinations of gnathopod forms. Allocation of all landhoppers to these two taxa would cause the perpetuation of two very large, poorly defined genera in which much more coherent subgroups could be identified. Recent work (Bousfield, 1971; Hurley,

1975a; Friend, 1979; Friend, in MS) indicates the existence of locally endemic groups of species, which, in recognition of the significance of different characters in the terrestrial arena of evolution, should be given generic rank. This policy has been followed in the subsequent systematic section, and results in a more satisfactory arrangement of the landhoppers treated.

KEY TO THE TERRESTRIAL AMPHIPODS OF MAINLAND TASMANIA

This key also applies to the offshore islands of Tasmania, excluding King Island and the eastern Bass Strait islands.

1. Gnathopod 1, hand subchelate, small; palm lateral, subequal to or longer than dactyl; some pleopods biramous and setose....2
 Gnathopod 1, hand simple, or palm, if present, oblique and either strongly exceeded by dactyl or hand swollen, much larger than hand of gnathopod 2.....5
- 2.(1) Gills all of similar size, basically sac-like.....3
 Gills of grossly unequal size, anterior and posterior pairs largest; posterior pair convoluted, lobate.....
*Neorchestia plicibrancha* sp.n.
- 3.(2) All pleopods long, slender, biramous, setose and subequal; antenna 1 short, just exceeding distal end of penultimate peduncular segment of antenna 2; epimeral plates converging beneath body, forming ventral slit through which pleopods protrude.....(*Orchestiella*)...4
 Pleopods 1 and 2 biramous and setose, third pair reduced to small stumps; antenna 1 long, almost reaching distal end of last peduncular segment of antenna 2...*Tasmanorchestia annulata* sp.n.
- 4.(3) Body anteriorly hunched, giving "teardrop" appearance (Figure 3.7); appendages extremely short; body cuticle hard, difficult to pierce with a needle..... *Orchestiella quasimodo* sp.n.
 Body of normal landhopper shape; appendages fairly short, body cuticle not unusually hard..... *Orchestiella neambulans* sp.n.
- 5.(1) All three pairs of pleopods biramous and setose.....6
 One or more pairs of pleopods reduced to vestigial stumps, sometimes extremely small, difficult to find, but always present.....8

- 6.(5) Gill of peraeopod 6 large, convoluted, with a large rounded posterior lobe.....(*Mysticotalitrus*)...7
 Gill of peraeopod 6 long, slender, anseriform^{*}, with a large subdistal posterior incision (Figure 3.1) *Arcitalitrus* sp.S.
- 7.(6) Hind corners of epimeral plates 2 and 3 sharp; telson with marginal and apical spines.....*Mysticotalitrus crypticus* sp.n.
 Hind corners of epimeral plates 2 and 3 rounded; telson with apical spines only.....*Mysticotalitrus tasmaniae* (Ruffo)
- 8.(5) Antenna 1 long, reaching more than halfway along last peduncular segment of antenna 2; telson with apical spines only; hind margin of segment 2, peraeopod 7, meeting main trunk of segment some distance above lower edge of segment i.e. posterodistal lobe absent. (e.g. Figure 3.30)....(*Tasmanian Austrotroides*)...9
 Antenna 1 short, only reaching or just exceeding distal end of penultimate peduncular segment of antenna 2; telson with marginal as well as apical spines; hind margin of segment 2, peraeopod 7, meeting main trunk of segment at lower edge of segment i.e. posterodistal lobe present (e.g. Figure 3.50).....
(*Keratroides*)...11
- 9.(8) Outer ramus of uropod 2 with margins naked; peraeopod 6 gill margins distally crenate (Figure 3.28).....
 *Austrotroides leptomerus* sp.n.
 Outer ramus of uropod 2 with marginal spines; peraeopod 6 gill margins not distally crenate.....10
- 10.(9) Gill of peraeopod 6 strongly incised posteriorly, forming a neck proximal to pointed distal lobe (Figure 3.24); telson bearing two large spines and two small spines near the apex; gnathopod 1, segment 6 slender, narrowing gently to very small oblique palm (Figure 3.23); body slender, legs very long, hind margin straight..... *Austrotroides longicornis* sp.n.

- Gill of peraeopod 6 hardly incised posteriorly (Figure 3.32);
 telson bearing two small spines only, near apex; gnathopod 1,
 segment 6 swollen, hind margin convex, palm not short (Figure
 3.31); body and legs not excessively long or slender.....
 *Austrotroides maritimus* sp.n.
- 11.(8) Epimeral plate 3 the longest, front corner sharp below, lower
 margin deeply concave (Figure 3.62), third plates usually
 curving beneath the body..... *Keratroides angulosus* (Friend)
 Epimeral plate 3 with rounded front corner, lower margin
 slightly concave, third plates flat.....12
- 12.(11) First and second pleopods broad, bearing broad rami with
 long setae, first pleopod biramous, second uniramous; third
 pleopod a small stump; antenna 2 short, shorter than head and
 first three body segments; head dorsally strongly rounded, eye
 small (width about 1/5 head length)..... *Keratroides albus* sp.n.
 Pleopods slender, vestigial, rami reduced to small papillae if
 present; long setae only found on narrow pleopods of some first
 instar specimens; antenna 2 much longer than head and first
 three body segments; head only gently dorsally rounded, eye
 width about 1/3 head length.....13
- 13.(12) Third epimeral plate deeper than second, front corner rounded,
 lower margin concave; gill of peraeopod 6 anseriform, narrowing
 distally, with a slender, linear distal extension (Figure 3.48).
 *Keratroides vulgaris* (Friend)
 Third epimeral plate just shallower than second, front corner
 rounded, lower margin slightly concave; gill of peraeopod 6
 anseriform, narrowing distally right to blunt apex, distal margins
 crenulate (Figure 3.57)..... *Keratroides pyrensis* sp.n.

Third epimeral plate strongly exceeded by second, front corner rounded, lower margin almost straight; gill of peraeopod 6 anseriform, distally incised, forming a distinct posterior lobe (Figure 3.52).....*Keratroides rex* sp.n.

* like the head, neck and upper body of a goose, in lateral view

Unless otherwise stated in the caption, the labelling of drawings in Figures 3.1 - 3.62 is as follows:

UL	upper lip
LL	lower lip
Rt Md	right mandible
Lft Md	left mandible
Mxl&2	maxilla 1 and 2
Mxpd	maxilliped, medial and lateral (dorsal and ventral) views
OP	outer plate of maxilliped, lateral view
PD	distal segments of maxilliped palp, medial view
Gnl&2	gnathopod 1 and 2
P3-7	peraeopod 3 - 7
O2-5	oöstegite of gnathopod 2 - peraeopod 5
G2-6	gill of gnathopod 2 - peraeopod 6
P11-3	pleopod 1 - 3
U1-3	uropod 1 - 3
Tel	telson

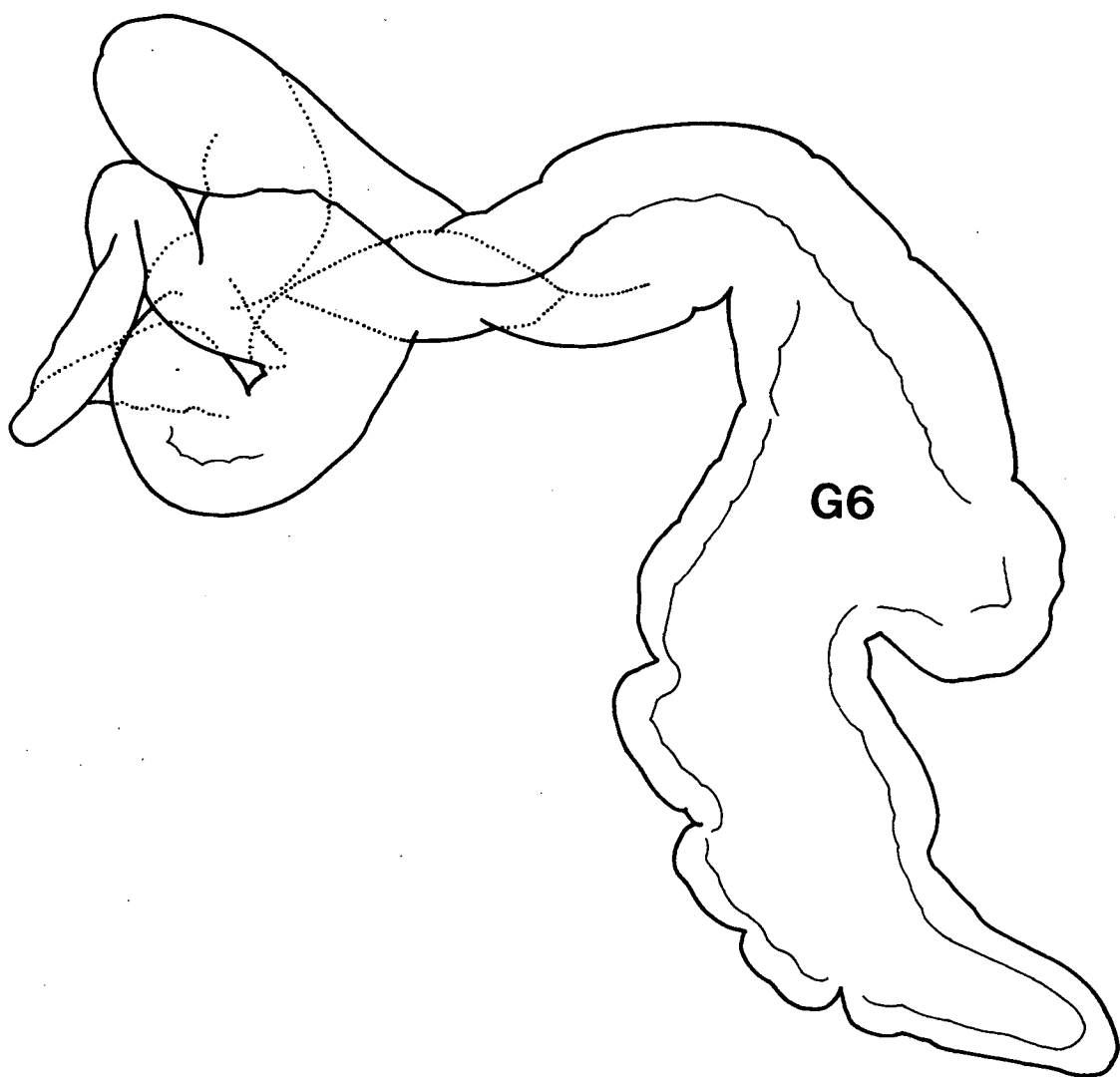


Figure 3.1 *Arcitalitrus* sp.S, ♀ 13.0 mm , Hunter I. (sample 7817-1).

Genus *Orchestiella*, gen. nov.

Diagnosis.

Small, plesiomorphic, sexually dimorphic landhoppers characterised by short first and second antennae, maxilliped with palps stout, lateral lobes broad with strong spine-groups, segment 4 unobscured; ♀ gnathopod 2 broad, stubby, mitten-shaped, ♂ gnathopod 2 hand enlarged, segment 6 broad-ovate; gills sac-like, subequal; pleopods long, slender, biramous, subequal; uropods 1 and 2 sexually dimorphic. Other features include maxilliped inner plate bearing many plumose setae, terminal spine-teeth small and subequal; gnathopod 1, segment 6 linear in ♀, distally broadening in ♂, posterior blisters better developed in ♂. Gnathopod 2 of ♀, segment 6 without anterior spine-groups, terminal lobe large, dactyl inclined across segment. Gnathopod 2 of ♂ strong, palm oblique, dactyl distally curved. Oöstegites narrow with long slender apical setae. Peraeopod 6 longer than 7, terminal spines of dactyls very short.

Type species: *Orchestiella neambulans* sp.n.

Other species: *O. quasimodo* sp.n.

Remarks

The species of this genus exhibit more plesiomorphic features than any other Tasmanian landhoppers, notably with respect to the mouthparts, gills, pleopods and gnathopods. Even so, there is already divergence from the morphology of the beach hoppers in the form of the maxilliped palp, with its unmasked fourth segment, relatively poorly setose, slender oöstegites and slender antennae.

An interesting feature of the genus is the presence of sexual dimorphism in the form and spination of the first and second uropods. No purpose for this is yet apparent, but this phenomenon has been recorded previously in two freshwater species from New Caledonia, *Orchestia pusilla* Chevreux and the closely related *O. starmuhlneri* Ruffo and Paiotta (Ruffo and Paiotta, 1972). Sexually dimorphic uropods in talitrids have been reported more recently by Friend (in MS; see Appendix) in the terrestrial genus *Agilestia* from eastern Australia.

Orchestiella gen. n. differs from *Agilestia* in having all pleopods subequal and with only two coupling spines on each, gills all of similar size, oöstegites with apical setae only, gnathopod 2 in the female with no spine-groups on the anterior margin of segment 6 (besides at the dactylar hinge) and gnathopod 2 in the male with a short, broad, hand.

The name of this genus means "*little Orchestia*".

Orchestiella neambulans, sp.n.

Figures 3.2 - 3.6

Types:

Holotype ♀; E. side of Olga R. valley, S.W. Tasmania, LGRSS (Lower Gordon River Scientific Survey) transect 7R, 1925 m. Top of a small hill at pit 45. UGR 8012-028606. Coll. JAF (see Appendix I for collectors) 18.ii.1976 (8012-32). Allotype ♂; S. side of Lyell Highway, just E. of King William Saddle, Tasmania. Ex litter, *Nothofagus* stand. UGR 8113-278261. Coll. JLH, TMW, GB, LC, JAF. 19.ii.1974 (8113-12). Paratypes 9 ♂♂, 16 ♀♀, (4 ovig.), 12 imm.; same data as holotype.

Other material examined: TASMANIA:

[number of specimens shown in brackets; full data listed under collection number in Appendix I. First four figures of collection number refer to Universal Grid prefix (Tasmap 1:100,000 series sheet number)]

7815-14(1)

7914-8(2)

7915-14(1)

8012-1(5), -2(7), -3(3), -18(6), -20(2), -21(1), -23(7), -26(24),
-31(6), -33(10), -42(1), -47(4), -48(1), -54(18), -60(6), -62(9)

8013-14(several) -19(1), -20(5), -22(55), -24(46), -25(2), -39(3)

8014-7(3), -9(9), -12(4), -13(1)

8112-10(2)

8113-12(7)

Diagnosis.

A small, sexually dimorphic landhopper, of the genus *Orchestiella* with large eyes, short antennae 1, fairly normal body shape, oöstegites present on gnathopod 2, long slender, subequal, biramous pleopods, epimeral plates deep, converging beneath the body, uropods 1 and 2 sexually dimorphic.

Description.

Female:

Length 6.8 mm, with no eggs [2-5], variation in a number of specimens shown in square brackets. Body moderately deep, epimeral plates converging distally, forming a narrow ventral slit through which pleopods 2 and 3 protrude.

Head deeper than long, eye large, about two-thirds head length, round, less pigmented at periphery. Antenna 1 quite short, reaching $1/5$ the length of fifth segment of antenna 2 peduncle, flagellum four-segmented, [3-4], shorter than peduncle. Antenna 2 short, as long as the head and first three peraeon segments together; peduncular segment 5 not as long as segments 3 and 4 together; flagellum of 8 segments [3-8], each bearing four groups of 2-3 long setae; distal segment long with a terminal brush of setae.

Upper lip narrow, deep, stiffly pilose apically. Lower lip narrow, deep, strongly pilose on inner shoulders, apical hairs long, throat margins pilose. Left mandible with 6-cusped incisor, lacinia mobilis 4-toothed, molar 18-striate. Right mandible 4-cusped, lacinia bearing a distal crenate surface. Maxilla 1, inner plate very slender, narrowing distally, outer margin pilose, terminal setae short; outer plate slender, narrowing distally, apical spine-teeth slender, dentition formula (number of teeth on apical spines, from outer to inner side) 2-0-0-2-5-2-4-5-5; palp situated at middle of outer margin, with its outer margin pilose. Maxilla 2, plates slender, apical spines tall, curved inward, inner plate bearing 12 spines, 5 small plumes and two proximal plumose setae.

Maxilliped inner plate narrowing distally to truncate apex; outer two spine-teeth subequal, inner smaller, all obscured by numerous long plumose setae; inner margin provided with 6 plumose setae. Outer plate apex broadly rounding, with an outer subterminal plumose seta, submarginal

spine-groups fairly strong. Palp broad, short, lateral lobes of segments 2 and 3 strong, projecting inwardly, bearing numerous slender spines, fourth segment not masked by lobe of third, distinct, conical.

Gnathopod 1, coxal plate rounded below, inner shelf weak, with two spines; segment 2 linear, anterior margin bearing two spines. Segment 4 spinose posteriorly with a weak blister. Segment 5 longer than 6, with a very weak posterior tumescence; segment 6 narrow-linear, bearing a few spines, palm short, transverse, not exceeded by closed dactyl.

Gnathopod 2, coxal plate deeper than broad, smoothly rounded below, spinose; posterior process distal, strong, blunt. Gill broader but not longer than others, sac-like, proximally twisted; oöstegite longer than segment 2, narrow, curved anteriorly with nine long slender setae near the apex. Segment 2 slightly broadening distally, with strong anterior expansion forming an anterodistal lobe. Segment 4 with a fairly strong posterior lobe. Segment 5 subequal to 6, posterodistally bearing a deep tumescence, weakly spined. Segment 6 broad, medial spine-row weak, distal lobe strong, minute dactyl steeply inclined posteriorly.

Peraeopod 3, coxal plate subsquare, posterior process very prominent, acutely rounded. Gill longer than segments 2 and 3 together, sac-like, proximally twisted; oöstegite as in gnathopod 2, with eleven long slender setae near the apex. Segment 2 poorly spinose, narrower in the middle than at the ends. Dactyl short, terminal spine small.

Peraeopod 4, coxal plate broader than deep, lower margin slightly convex, posteriorly extended to broadly acute corner; posterior process vestigial. Oöstegite almost straight, eleven apical setae present. Otherwise like peraeopod 3.

Peraeopod 5 short, segments 2-7 just over half as long as in peraeopod 6, anterior lobe shallow, smoothly rounded exceeding shallow posterior lobe, both very weakly spinose below. Gill as in peraeopod 3, oöstegite just shorter than, but twice as broad as anterior ones, sharply

narrowing distally to subacute apex bearing seven long slender setae. Segment 2 broad-ovate, weakly serrate and spinulose posteriorly. Segments 4-6 short, slender, moderately spinose; dactyl small, terminal spine short and curved.

Peraeopod 6, anterior coxal lobe very shallow, posterior lobe strongly rounded, spinulose below. Gill the longest, narrow, sac-like, twisted proximally. Segment 2 subovate, moderately expanded behind, spinulose, distal lobe present but shallow. Segments 4-6 slender, spinose. Dactyl long, slender, curved, terminal spine very short, straight.

Peraeopod 7 just shorter than 6, coxal plate shallow, smoothly rounding below, with several spinules on hind margin. Segment 2 broader than long, expanded behind to weakly serrate and spinulose margin; distal lobe broad and shallow. Segments 4-6 slender and moderately spinose. Dactyl long, slender, curved, terminal spine short, straight.

First epimeral plate, lower margin oblique, hind margin serrate and spinulose. Second epimeral plate large, lower margin smoothly rounded, posterior corner slightly produced, blunt, hind margin slightly sinuous, spinulose. Third plate smaller, hind corner more produced, sharp, hind margin sinuous, spinulose.

Pleopods long, slender, subequal, biramous, thickness of peduncles decreasing posteriorly, peduncle of first shorter than in second and third, two coupling hooks on each peduncle. Numbers of segments of inner and outer rami in first pleopod, 15 and 12, in second pleopod, 16 and 12, in third pleopod, 13 and 11 respectively; inner rami always longer than outer.

Uropod 1, peduncle slender, with one large inner and three outer marginal spines, apical spine long, proximally stout. Rami slender, subequal, shorter than peduncle, outer ramus bearing one marginal spine near the midpoint, inner ramus with five marginal spines. Uropod 2 peduncle short, bearing one outer and four inner marginal spines, and

a short apical spine. Rami slender, upper margin corrugated, outer longer than inner; outer ramus armed with two marginal spines, inner ramus with five spines evenly spaced along the proximal two-thirds, then two spines very close together near the distal end of the margin. Uropod 3, peduncle slender, narrowing distally, bearing one large spine. Ramus slender, apically provided with one large and two small spines.

Telson narrow, apex entire but two lobes visible; one apical spine on each side.

Male:

5.9 mm long. Antenna 1 flagellum four-segmented [3-4], antenna 2 flagellum of seven segments [3-7].

Gnathopod 1 as in ♀, but posterior lobes deeper. Segment 6 shorter than 5, broadening distally, postero-distal lobe projecting distally past closed dactyl, medial surface bearing numerous spines. Dactyl closing on short palm which is defined posteriorly by tumescent lobe, past which dactyl does not project.

Gnathopod 2, coxal plate, gill similar to ♀. Segment 2 strong, convex behind, expanded and spinose anteriorly. Segment 6 ovate, palm oblique, straight, lined with small spines, defined by a larger spine. Dactyl strong, distally curved, exceeding palm and closing in a medially-placed cleft near the palmar angle.

Uropod 1, peduncle like that of ♀, rami slender, subequal, outer marginally bare, inner bearing a row of seven evenly-spaced spines on slightly thicker part of ramus, between one-sixth of the total length from the proximal end and just past midway along the ramus. Uropod 2, peduncle short, with four outer and two inner marginal spines, no apical spine; rami subequal, outer spined as ♀, inner with a short even row of four spines on a swelling in the upper margin just proximal of a constriction halfway along the upper surface of the ramus. Uropod 3 as in ♀ but bearing two peduncular spines.

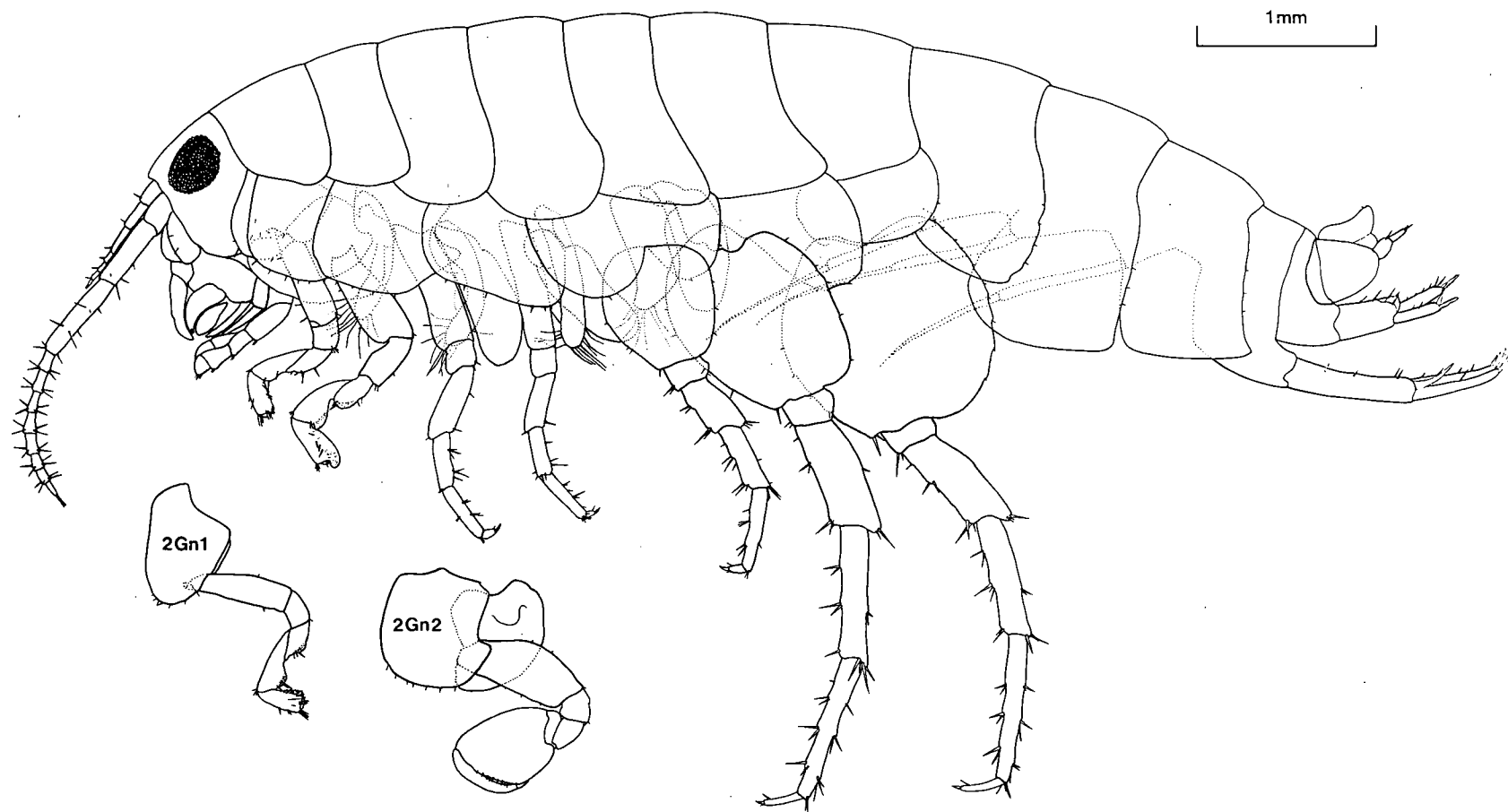


FIGURE 3.2 *Orchestiella neambulans* gen. et sp.n., holotype ♀. 2, allotype ♂.

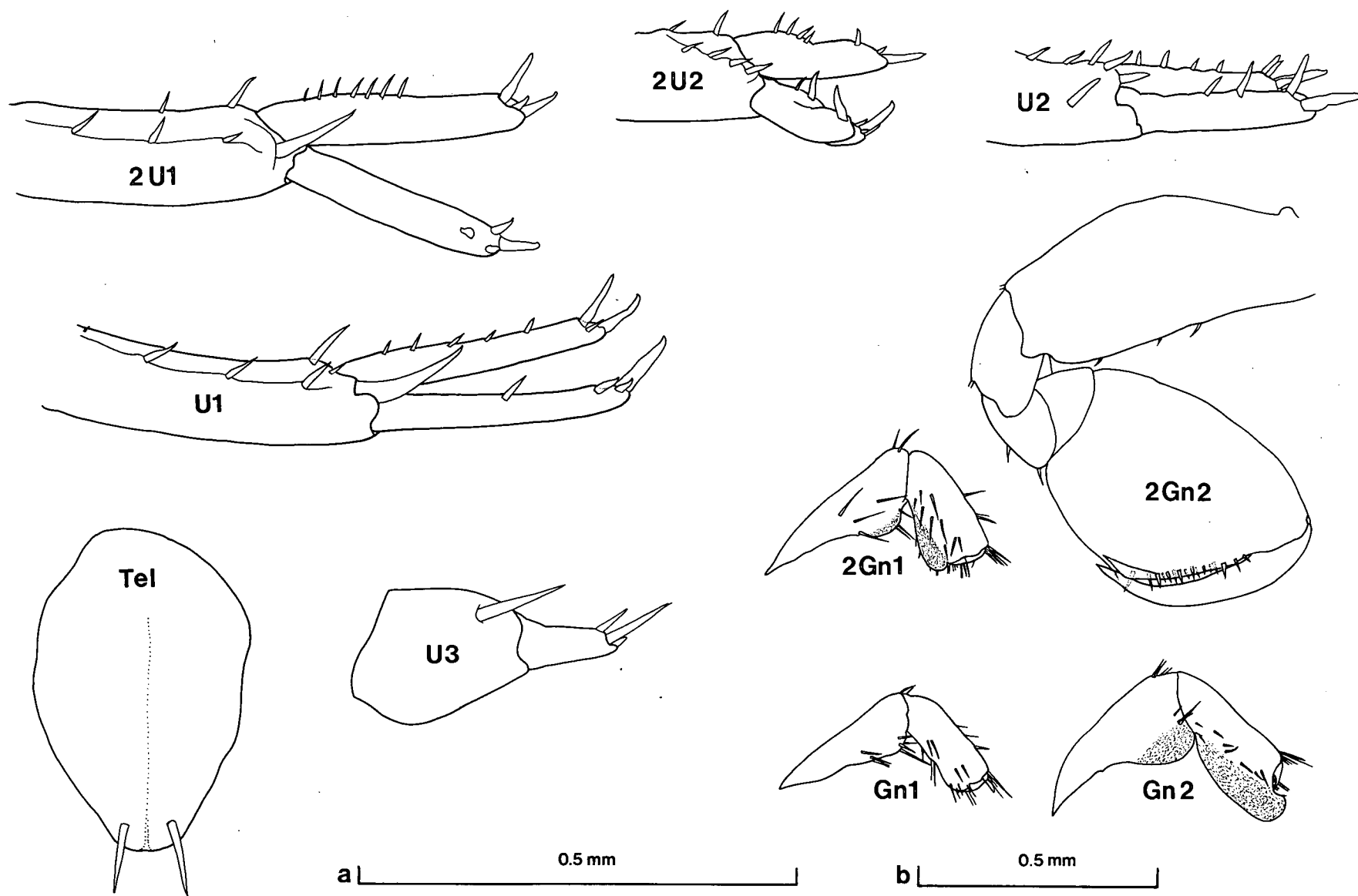


FIGURE 3.3 *Orchestiella neambulans* gen. et sp.n., holotype ♀. 2, allotype ♂. Scale a; Gn1&2, 2Gn1&2, U1&2, 2U1&2. Scale b; Tel, U3.

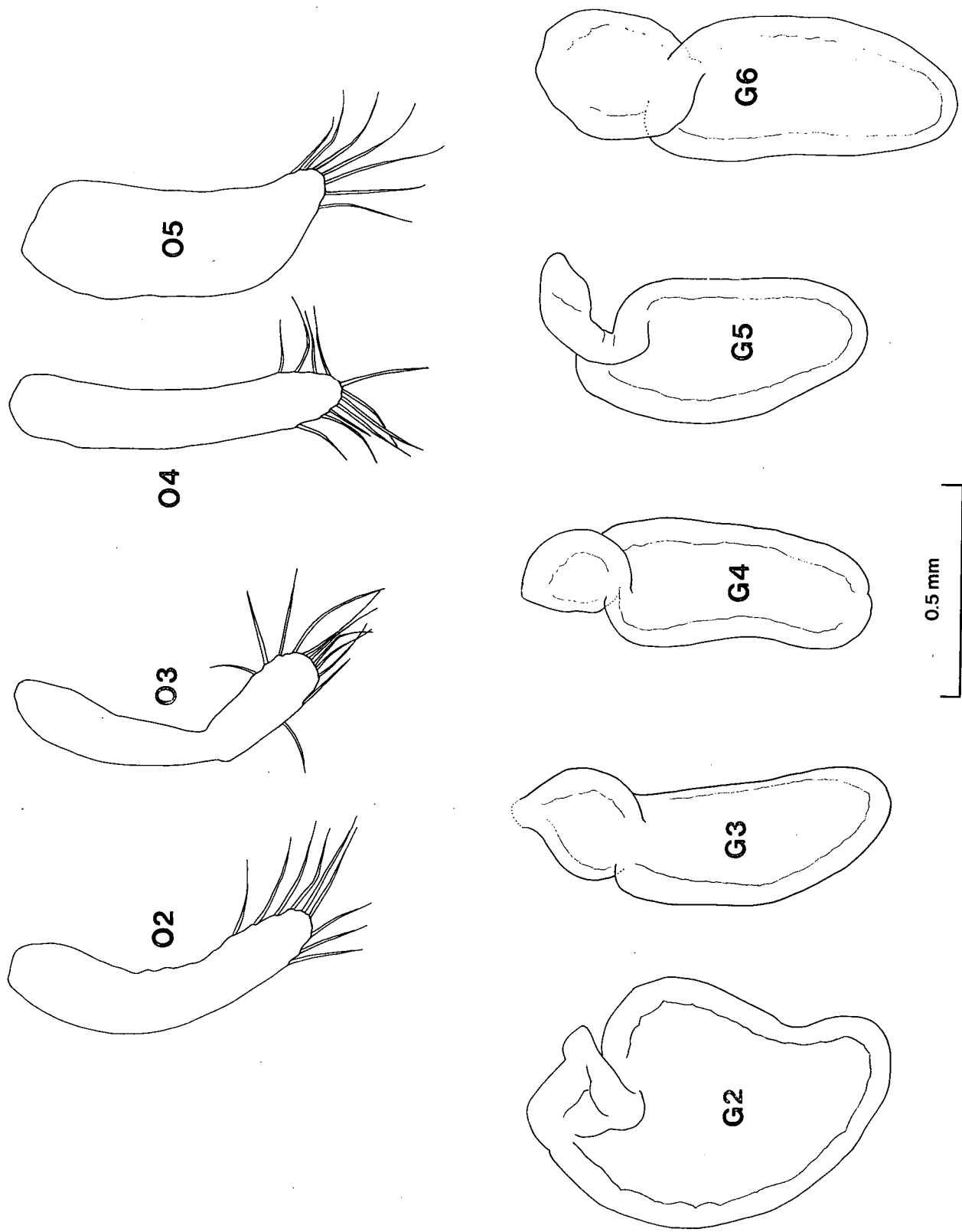


FIGURE 3.4 *Orchestiella neambulans* gen. et sp.n., holotype ♀.

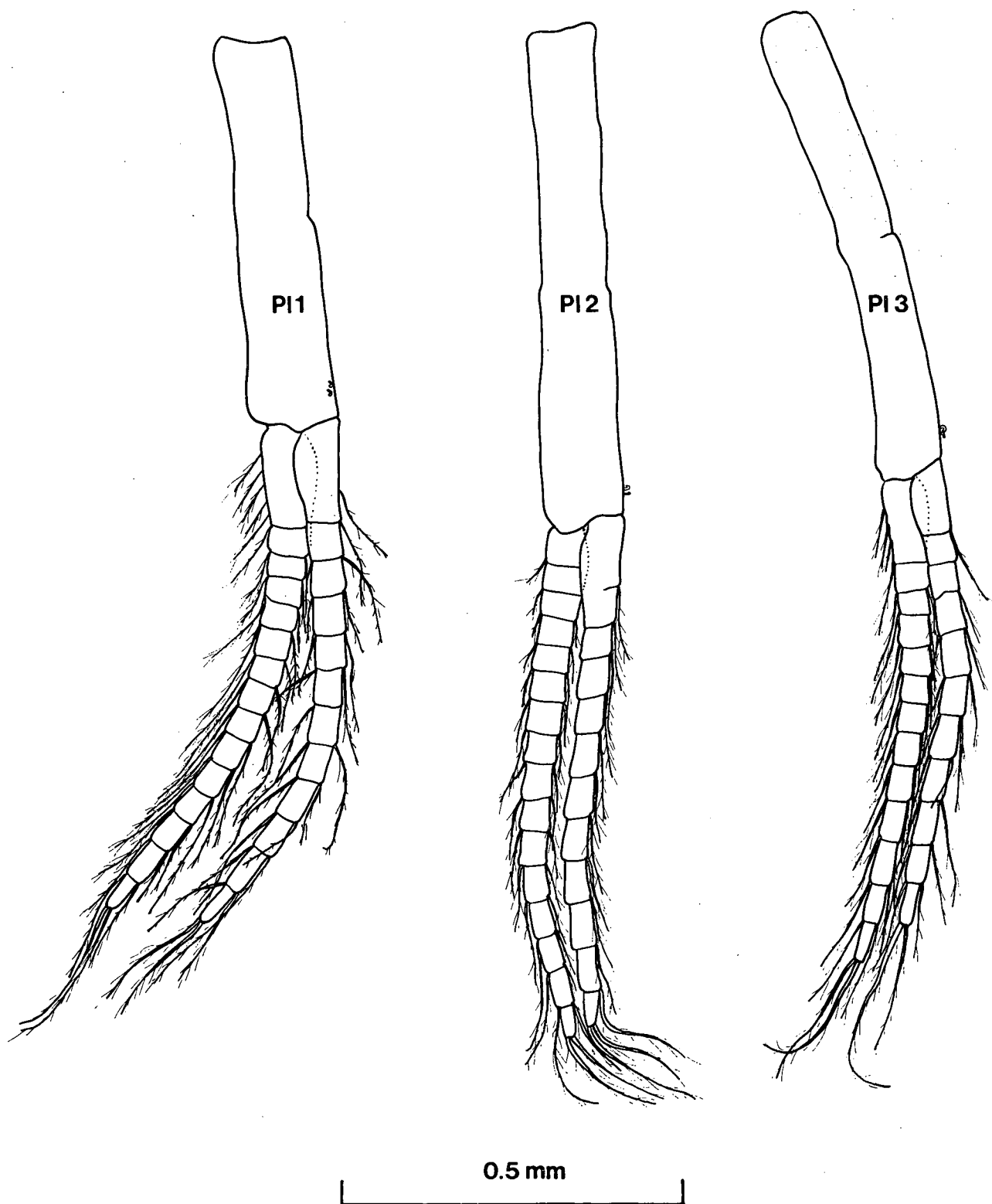


FIGURE 3.5 *Orchestiella neambulans* gen. et sp.n., holotype ♀.

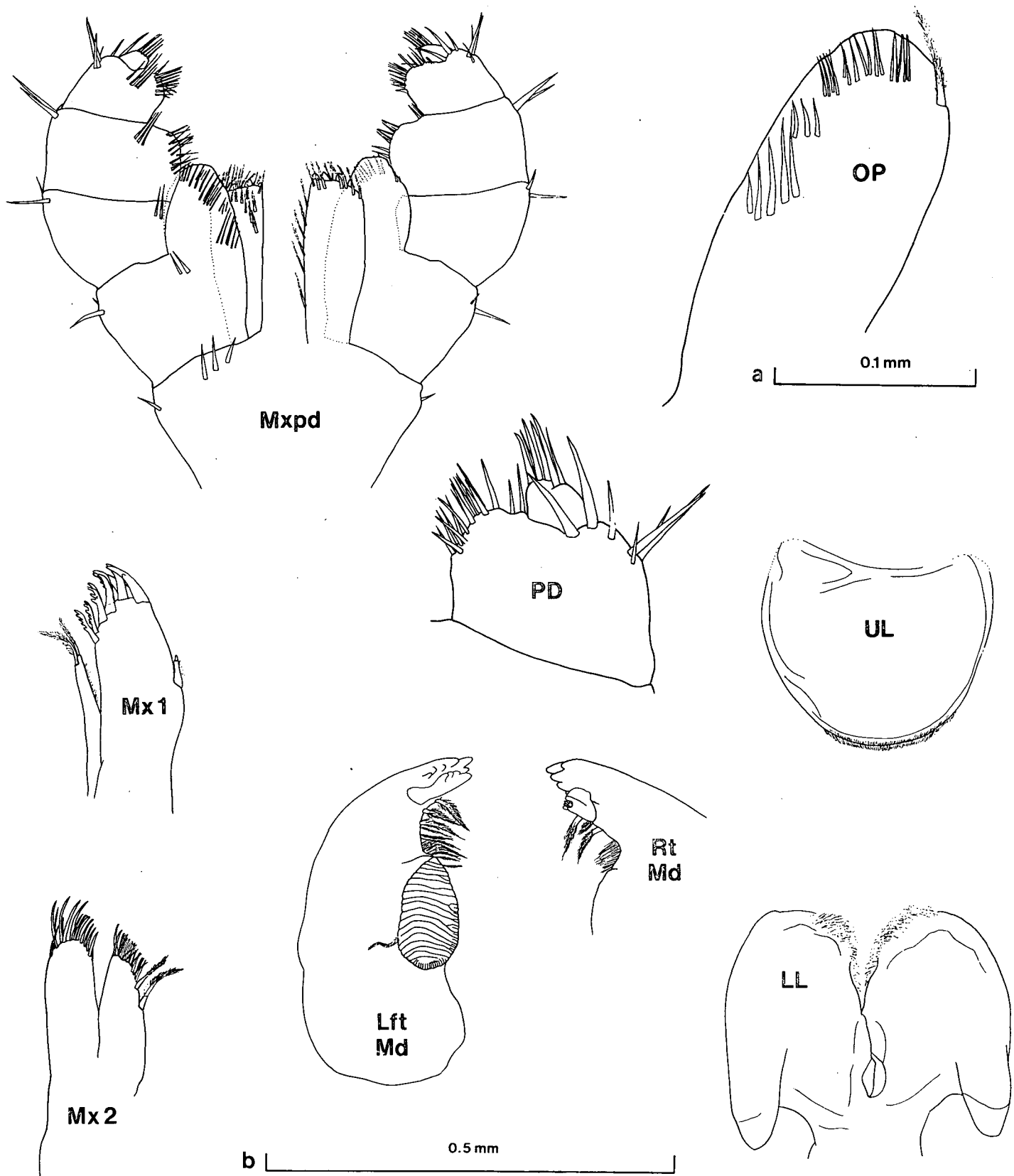


FIGURE 3.6 *Orchestiella neambulans* gen. et sp.n., holotype ♀. Scale a; OP, PD. Scale b; Mxpd, Mx1&2, Rt Md, Lft Md, UL, LL.

Otherwise like ♀ but lacking oostegites and bearing paired ventral penes on peraeonite 7.

Remarks

Orchestiella neambulans sp.n. is found only in western Tasmania, where it is most abundant under *Leptospermum lanigerum*, a teatree species commonly associated with swampy ground.

Mature males are smaller than mature females; males with enlarged second gnathopods are rare in samples of this species. Wildish (1979) has predicted sex ratios biased towards the female in "primitive" land-hopper species; however this is the only Tasmanian species which appears to demonstrate this feature to any marked extent. *O. neambulans* sp.n. (and the following species) also possesses other characteristics anticipated by Wildish amongst the "primitive" group; small body size, low brood numbers and, assuming an annual life cycle, slow growth rate, although these three features are obviously very closely interrelated.

Cysts are often found on the gills of *O. neambulans* sp.n., especially along the margins. These were not fruitfully investigated, but appear similar to those reported by Barnard (1960) on *Talitrus toli* Barnard as due to protozoan infection.

The name of this species means "newly walking", in reference to its similarity in some features, to marine members of the Talitridae.

Orchestiella quasimodo, sp.n.

Figures 3.7 - 3.11

Types:

Holotype ♀ (ovig., 1 egg); S. side of Gordon River valley, S.W. Tasmania, LG^{ss}, transect 11A, 720 m. In litter under *Leptospermum* stand. UGR 8012-944830 Coll. JAF, 28.i.1976 (8012-18). Allotype ♂; Beside Old Hartz Track, at head of Arve R., W. of Taylor's Ridge. Ex litter from beneath *Richea pandanifolia*. UGR 8211-829146. Coll. JLH, AMMR, 24.viii.1973 (8211-9). Paratypes ♂, 8 ♀♀ (2 ovig.), 1 imm.; same data as holotype.

Other material examined: TASMANIA:

8012-6(2), -8(1), -10(3), -12(1), -14(1), -15(1), -20(1), -43(1),
 -44(2), -45(15), -46(9), -52(1), -53(2), -66(2), -67(26)
 8013-8(10), -9(4)
 8014-2(5), -8(4)
 8110-24(3)
 8210-7(2)
 8211-1(14), -2(1), -6(1), -9(16), -18(1)

Diagnosis

A very small, sexually dimorphic landhopper with a distinctive, anteriorly hunched body shape and hard body cuticle; this species also lacks ostegites on gnathopod 1 and has very short peraeopods, long, slender, subequal biramous pleopods, deep epimeral plates converging beneath the body, and sexually dimorphic uropods.

Description.

Female:

Length 5.2 mm, ovigerous, with 1 egg [1-3]. Body deep, peraeon

and pleon segments short. Antennae, gnathopods and peraeopods very short, cuticle relatively hard, epimeral plates converging distally, forming a narrow ventral slit through which pleopods 2 and 3 protrude.

Head as long as deep, largely masked posteriorly by coxa of first gnathopod. Eye large, round, diameter about half head length, less pigmented at periphery. Antenna 1 short, just exceeding fourth segment of antenna 2 peduncle, flagellum 3-segmented [3], shorter than peduncle. Antenna 2 very short, just longer than head and first peraeon segment together, peduncular segment 5 short, equal to segments 3 and 4 together; flagellum of six segments [4-6], mostly bearing 4 groups of 2-3 very short bristles; distal segments long, with a brush of terminal setae.

Upper lip narrow, apex smoothly convex, strongly pilose distally, hairs relatively long. Lower lip deep, narrow, inner shoulders strongly pilose, apical hairs long, throat margins lightly pilose. Left mandible, incisor 5-cusate, lacinia mobilis 5-cusate, molar 17-striate. Right incisor 5-cusate, lacinia with 3 cusps, one a long process. Maxilla 1 inner plate slender, terminal setae long, inner longer than outer; outer plate narrow, outer apical spine-teeth broad, inner slender, dentition formula 2-2-0-3-2-4-3-4-4; palp 2-jointed, set just distal of midpoint of outer margin. Maxilla 2 plates slender, terminal spines long, curved inwards, inner plate with row of short sub-terminal plumose setae, outer margin of outer plate and inner margin of inner plate setose.

Maxilliped, inner plate narrowing slightly to truncate apex which bears short rounded spine-teeth, inner two subequal, well supplied with plumose setae which exceed and mask spine-teeth; inner margin with six plumose setae. Outer plate, apex broadly acute, submarginal spine-rows strong, outer margin with 3 distal plumose setae. Palp broad, short, fourth segment distinct, conical, lateral lobes on segments 2 and 3 strong, projecting inwards, bearing numerous slender spines.

Gnathopod 1, coxal plate rounded below, lightly spinose; inner

shelf weak, with 8 spines. Segment 2 linear, with three anterior spines and one posterodistal spine. Segment 4 spinose posteriorly, with a weak blister. Segment 5 longer than 6, posterior margin tumid and spinose. Segment 6 slightly widening distally, palm short, transverse, not exceeded by closed dactyl, bearing groups of stiff setae posteriorly and anterodistally. Dactyl slender.

Gnathopod 2, coxal plate very deep, posterior process short, sharply rounding. Gill the largest, sac-like but twisted proximally; oöstegite absent. Segment 2 broad, slightly expanded distally with 2 small anterior marginal spines, segment 4 shorter than 3, with a posterior blister. Segment 5 a little longer than 6, posterodistally tumescent, segment 6 with a blunt apical lobe. Dactyl subapical, almost transverse.

Peraeopod 3 very short, coxal plate deep, posterior process prominent, sharply rounded. Gill narrow, sac-like, proximally twisted; oöstegite long, tapering distally, with 6 long setae near apex. Segment 2 slightly curved anteriorly, dactyl short, stout.

Peraeopod 4 similar to 3, except coxal plate subrhomboid, posterior process very shallow, distal and broadly rounded; oöstegite with 5 setae.

Peraeopod 5, anterior coxal lobe shallow, posterior lobe much deeper, broadly rounded distally, bearing a single small spine. Gill sac-like, twisted proximally; oöstegite short, broad, curved anteriorly, bearing four apical setae. Segment 2 broad, ovate, anterior margin armed with short, stout spines, posterior margin nearly smooth, dactyl short.

Peraeopod 6, posterior coxal lobe deep, distal margin smoothly rounded. Gill sac-like, proximally twisted, larger than that of peraeopod 5. Segment 2 subovate, anterior margin bearing short, stout spines, posterior margin smooth, bearing one spinule and no distal lobe. Segments 4-6 short, armed with short, stout spines; dactyl stout, nail short, curved.

Peraeopod 7, coxal plate deep, rounded below; segment 2 very broad, anterior margin broadly convex, set with short, stout spines, posterior margin greatly expanded, broadly rounded, spinulose, distal lobe shallow. Segments 4-6 short, normally spinose; dactyl short.

Epimeral plates deep, spinulose behind, first rounded below, second and third with smooth lower margins, corners slightly produced, subacute. Pleopods long, slender, each with two coupling spines and well supplied with long plumose setae, biramous. First and second with subequal, 10-12-segmented rami and three plumose setae on outer peduncular margin. Third with inner ramus about half as long as outer, rami of five and nine segments respectively.

Uropod 1, rami subequal, shorter than sparsely spinose peduncle; outer ramus marginally smooth, inner ramus bearing two short marginal spines; peduncular apical spine simple, curve-tipped. Uropod 2 rami stout, subequal to peduncle, inner ramus bearing two marginal spines, outer, one; peduncle armed with a strong apical spine. Uropod 3, peduncle sub-cylindrical, with a dorsal pair of stout spines; slender ramus shorter, bearing two large and one small spine apically.

Telson narrow, with a group of three stout spines on each side of the cleft apex.

Male:

Length 4.2 mm. Antenna 1, flagellum of 3 segments [3], antenna 2, flagellum 5-segmented [4-5].

Gnathopod 1, coxal plate narrower than in ♀, inner shelf weak, with three spines, segment 2 with one anterior marginal spine, segment 5 with a deeper tumid lobe than in ♀. Segment 6 broadening distally, with a posterior lobe which extends distally and posteriorly behind the closed, stout dactyl.

Gnathopod 2, coxal plate distally rounded, segment 2 strong, posterior margin strongly convex near mid-point, segment 6 squarely

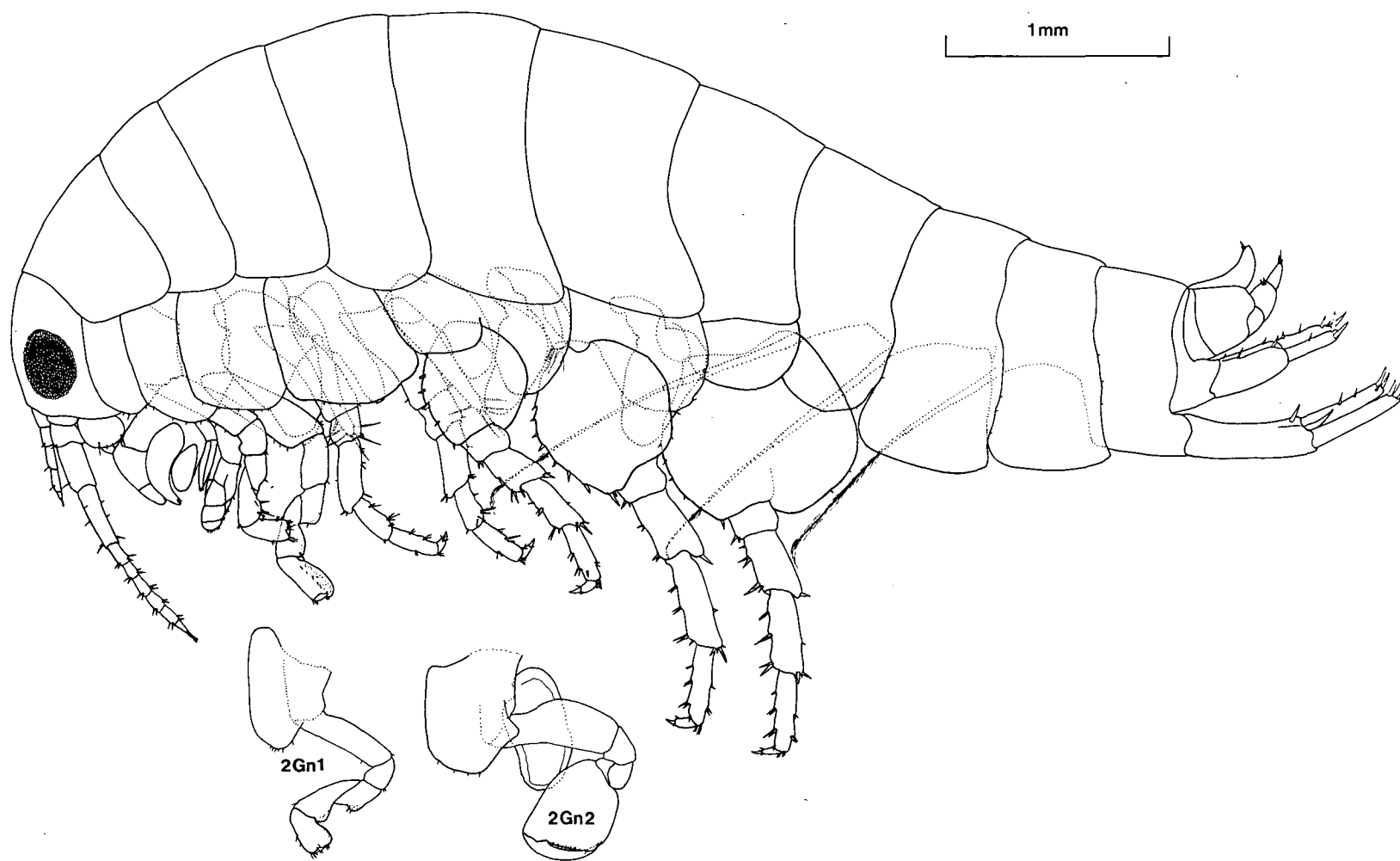


FIGURE 3.7 *Orchestiella quasimodo* gen. et sp.n., holotype ♀. 2, allotype ♂.

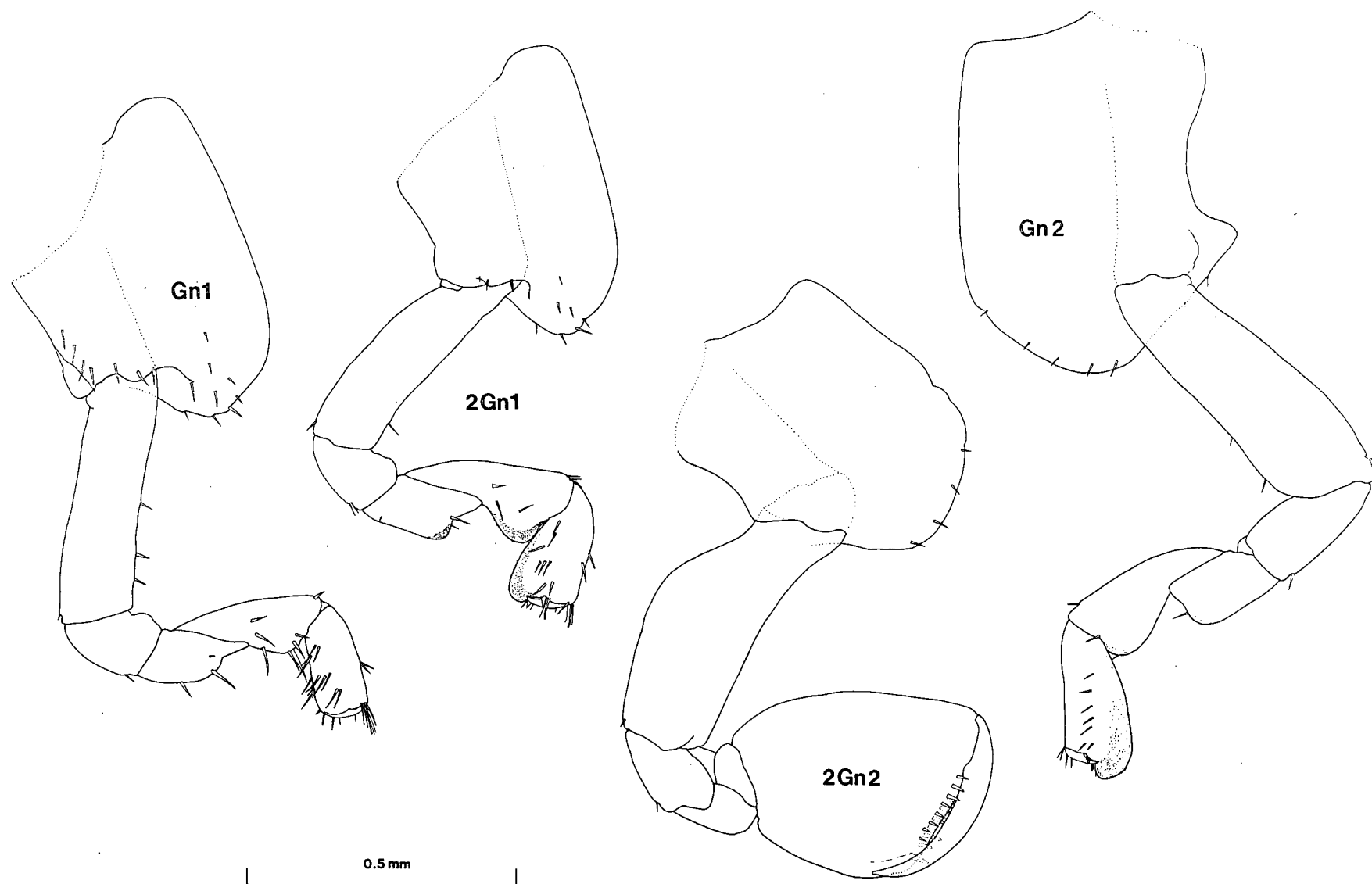


FIGURE 3.8 *Orchestiella quasimodo* gen. et sp.n., holotype ♀. 2, allotype ♂.

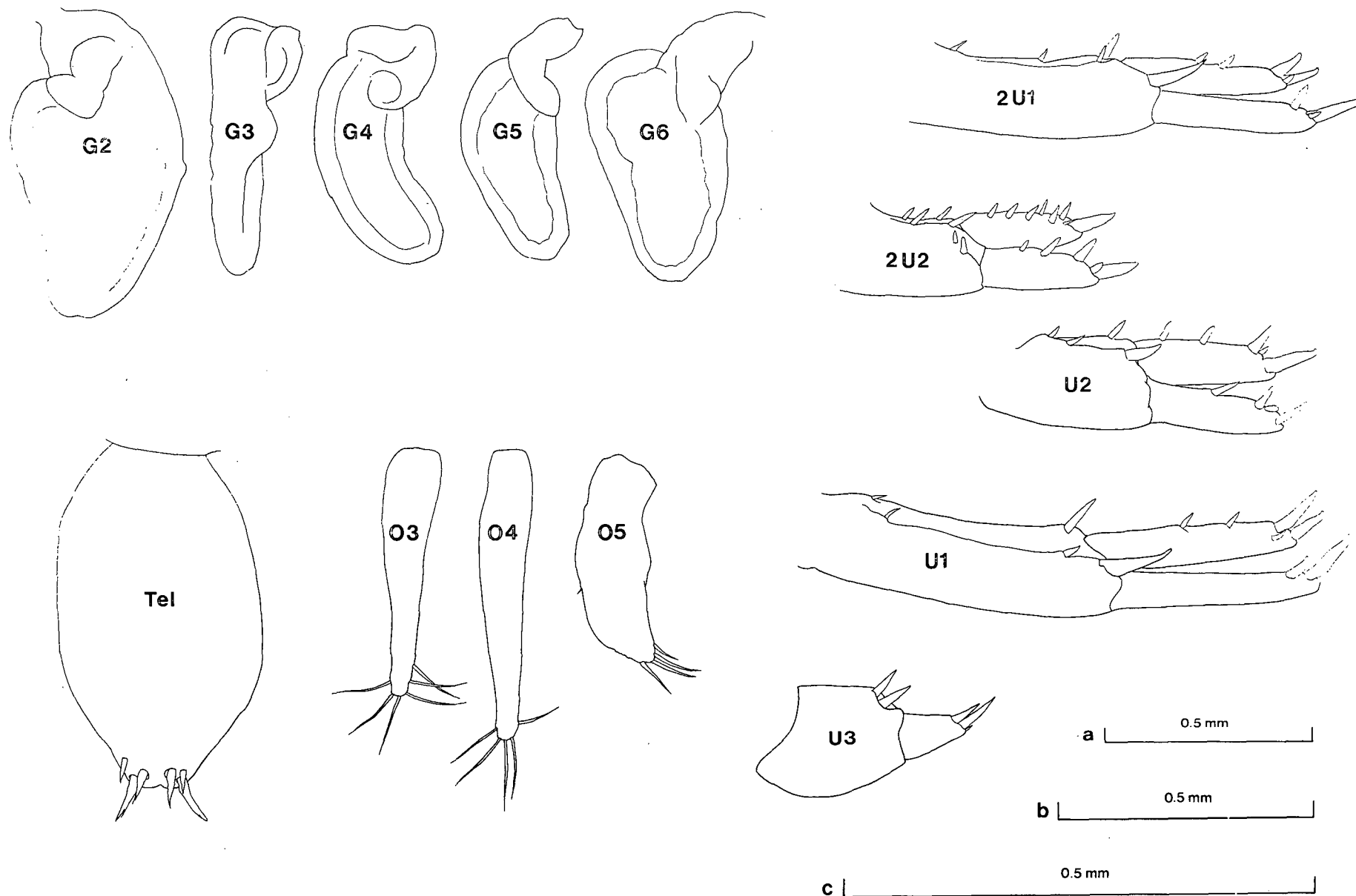


FIGURE 3.9 *Orchestiella quasimodo* gen. et sp.n., holotype ♀. 2, allotype ♂. Scale a; O2-5, G2-6. Scale b; U1&2, 2U1&2. Scale c; Tel, U3.

0.5 mm

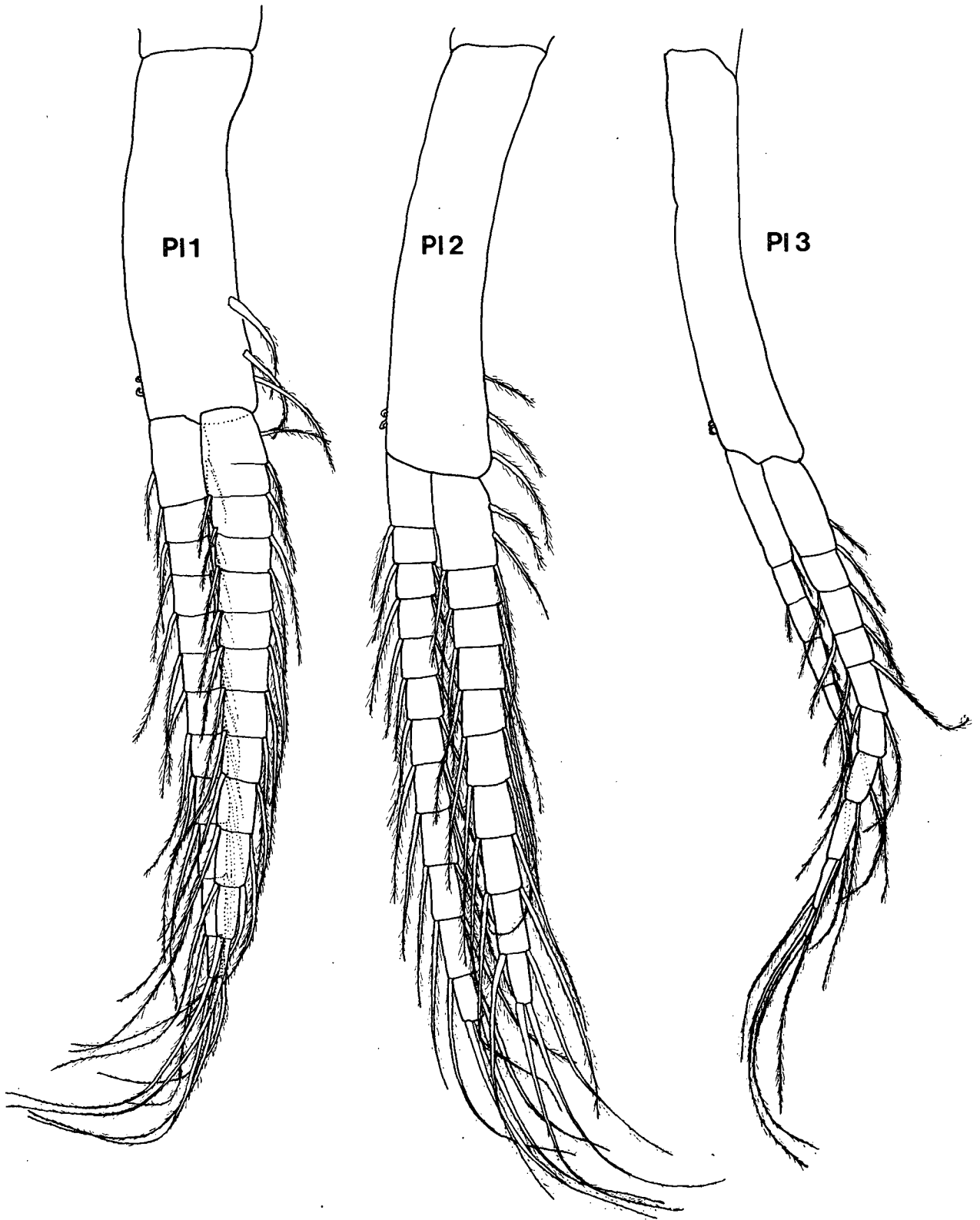


FIGURE 3.10 *Orchestiella quasimodo* gen. et sp.n., holotype ♀.

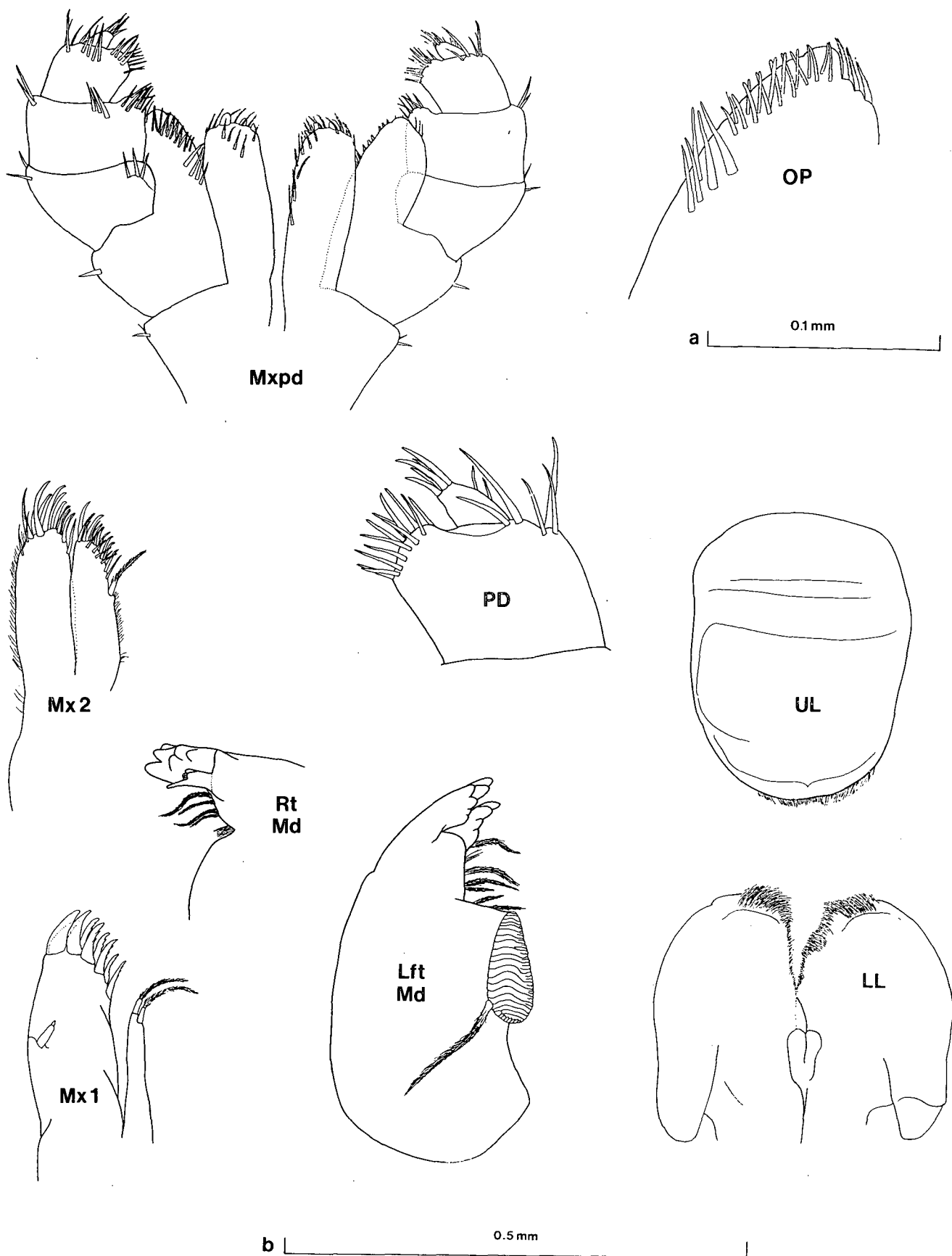


FIGURE 3.11 *Orchestiella quasimodo* gen. et sp.n., holotype ♀. Scale a; OP, PD. Scale b; Mxpd, Mx1&2, Rt Md, Lft Md, UL, LL.

ovate, palm slightly oblique, straight, evenly lined with short stout spines, posterior angle with a groove to accomodate the curved tip of the strong dactyl.

Uropod 2 more spinous than in ♀; peduncle bearing two more spines near apex, outer ramus with two marginal spines, inner with five.

Otherwise like ♀, but lacking oöstegites and bearing paired ventral penes on peraeonite 7.

Remarks

This species is quite similar to *O. neambulans* sp.n. but may be easily distinguished by its unusual body shape. The body segments are deep and extremely short anteriorly, resulting in a hunched appearance (hence the name *quasimodo*). The pleosome is laterally narrow, so the whole effect is one of apparent streamlining. In addition, the peraeopods are ridiculously short when compared to those of other land-hoppers, giving the amphipod a very distinctive facies. Otherwise, the extremely hard exoskeleton, the broader hand of male gnathopod 2, and the apically more spinose telson serve to differentiate *O. quasimodo* sp.n. from *O. neambulans* sp.n. Males with large second gnathopods are much more common in this species than in *O. neambulans* sp.n. Full-grown males of *O. quasimodo* sp.n. are smaller than full-grown females.

O. quasimodo sp.n. also appears most abundant in teatree woodland and swamps. These amphipods appear to favour hopping, using the strong pleosome as a means of locomotion; the very short legs are apparently not as well-adapted for walking as the long slender legs of many other leaf-litter species.

The very hard body cuticle of this small species is a unique feature amongst the Tasmanian amphipods. It is tempting to liken this feature to the thickening of the exoskeleton found in the Oniscoidea which allows much greater water retention. As *O. quasimodo* sp.n.

inhabits forests with an average annual rainfall of at least 1800 mm falling throughout the year, however, it is unlikely that the tendency to desiccate has been sufficiently strong to cause this radical adaptation. It is more probable that a hard body and a well-developed jumping ability together help avoid predation to a significant extent.

Genus *Tasmanorchestia*, gen. nov.

Diagnosis

Sexually dimorphic landhoppers with subchelate gnathopod 1 in both sexes, gnathopod 2 strongly subchelate in male with long curved dactyl; mitten-shaped in female, with segment 6 narrow, anterior margin naked to hinge of dactyl; antenna 1 almost as long as peduncle of antenna 2; maxilliped palp segments lobate with spinose inner margins, fourth segment partly masked by lateral lobe of segment 3; anterior and posterior gills larger than others, sac-like; pleopods reduced or vestigial; uropods similar in both sexes. Other features include broad oöstegites bearing long distal setae; upper and lower lips, maxilla 1 and 2 narrow; peraeopod 7 the longest, dactyls of peraeopods 6 and 7 long and slender with long terminal spines.

Type species: *Tasmanorchestia annulata*, sp.n.

Remarks

The features distinguishing this monotypic genus from *Agilestia* are the sharp distal lobe and lack of anterior marginal spine-groups on segment 6 of ♀ gnathopod 2, the partially masked fourth segment of the maxilliped palp, the ventrally unmodified peraeonite 1, the reduced or vestigial pleopods, and the sexually similar uropods 1 and 2.

Tasmanorchestia gen.n. differs from *Orchestiella* gen.n. in the possession of reduced or vestigial pleopods, an elongate sixth segment of ♀ gnathopod 2, the very oblique palm of the ♂ gnathopod 2, exceeded by the long dactyl, sexually similar first and second uropods, the hand of the ♂ gnathopod 1 not strongly lobate behind, and the more slender maxilliped palp and semi-masked fourth segment.

As no similar species have been found, the name of the genus alludes to the apparently restricted distribution.

Tasmanorchestia annulata, sp.n.

Figures 3.12 - 3.16

Types

Holotype ♀ (ovig., 2 eggs); Beside Strahan-Zeehan road, 4 km N. of Henty R. bridge, W. Tasmania, in *Pittosporum bicolor* litter. UGR 7913-592483. Coll. JAF, 29.x.1977 (7913-11). Allotype ♂; same data as holotype. Paratypes 3 ♂♂, 2 ♀♀; 2.2 km S. of 4-mile peg on Savage R. pipeline road. UGR 7915-523123. Coll. AMMR et al. 11.v.1975 (7915-3).

Other material examined: TASMANIA:

7719-1(2), -3(4)

7815-11(12), -12(2), -19(1)

7816-1(~100), -13(11), -17(14), -18(7), -19(11), -21(10), -22(17), -23(4)

7913-6(35), -7(50), -8(5), -11(6)

7914-1(4)

7915-4(2)

7916-2(10)

8011-3(4)

8015-5(3), -11(1)

8110-1(4), -2(3), -7(8), -8(1), -9(17), -10(9), -22(44)

Diagnosis

A sexually dimorphic landhopper with light and dark lateral body stripes, long first antennae, subequal gills, first and second pleopods with reduced rami and vestigial third pleopods.

Female:

7.9 mm long, ovigerous with 2 eggs. Body brown in life with light and dark transverse stripes. Head capsule longer than deep, eye

almost round, large, width over two-fifths head length. Antenna 1 long, reaching almost to the distal end of the peduncle of antenna 2, flagellum of six segments [3-8], shorter than peduncle. Antenna 2 relatively short, exceeding the length of the head and first three body segments together, segment 5 of peduncle long, longer than segments 2-4 together; flagellum of 13 segments [5-15], mostly long, with 4 groups of long bristles; last segment short with long terminal setae.

Upper lip deep, strongly pilose apically. Lower lip narrow, lateral lobes small, pilose on outer margins, inner shoulders stiffly pilose, sides of central trough lightly pilose on distal part only. Left mandible, incisor 5-cusped, lacinia mobilis 4-dentate, molar strong, 20-striate. Right mandible, incisor 5-toothed, lacinia mobilis 3-dentate. Maxilla 1, inner plate slender, inner terminal seta longer than outer; outer plate narrow, 2-segmented palp at broadest point, terminal spines slender, dentition formula 2-2-2-4-5-4-4-4-6.

Maxilla 2 plates slender, inner rather shorter than outer, terminal spines long, slender, distally curved, plumose seta at inner end of distal margin large, inner margin distally finely pilose. Outer plate as broad as inner, apical spines long and slender, outer margin distally bare, proximally pilose.

Maxilliped inner plate broadening distally to truncate apex which bears three short rounded spine-teeth, concealed among the six apical plumose setae; lateral surface bearing a group of six plumose setae, inner margin of medial side with five plumose setae. Outer plate, long, slender, apically rounded with three plumose setae set into the outer distal margin; submarginal spine-row double, strong, spines blunt. Palp fairly broad, spines on lateral face and inner margin small; segments 2 and 3 with lateral lobes, each set with a group of small spines; lobe of segment 3 half masking the rounded fourth segment, which bears four small apical spines.

Gnathopod 1, coxal plate broad, distally rounded, spinose; inner

shelf weak, spinose. Segment 2 linear, both margins weakly spined. Segment 4 with a barely perceptible posterior lobe. Segment 5 long, well spined behind, posterior tumid lobe very weak. Segment 6 much shorter than 5, almost linear, with small spines on the medial surface, anterior margin bearing two small spine-groups; palm transverse, covered with minute serrations, just exceeded by strong dactyl.

Gnathopod 2, coxal plate broad, lower margin smoothly rounded, spinulose, posterior process prominent, almost a right angle. Gill simple, kidney-shaped, broader and slightly longer than gills of peraeopods 3 and 4, oöstegite curved anteriorly, shorter than segment 2, apically rounded and bearing six slender setae. Segment 2 almost linear, fairly broad, weakly spinose. Segment 4 with a sharply rounded posterodistal tumescence, margins weakly spined. Segment 5 deep, very poorly spinose, posterior tumid lobe well-developed. Segment 6 as long as 5, slender, medial spines forming a dense distal group near the oblique dactyl; distal lobe long, apically quite pointed; anterior margin bearing spines only at the hinge of the dactyl.

Peraeopod 3, coxal plate broader than deep, lower margin almost straight, spinulose; posterior process prominent, subacute. Gill simple, sac-like, shorter than segment 2; oöstegite similar to but slightly longer than that of gnathopod 2, with six slender apical setae. Segment 2 broadening slightly distally, margins almost bare. Dactyl quite short terminal spine curved.

Peraeopod 4, coxal plate shallow, much broader than deep; lower margin slightly convex, spinulose. Gill as in peraeopod 3, oöstegite broader and longer, bearing eight setae near the apex. Segments 2 and 4 shorter than in peraeopod 3, limb otherwise similar.

Peraeopod 5, anterior coxal lobe very shallow, front and lower margins smoothly rounded, naked; posterior lobe longer, weakly spinulose, convex behind. Gill sac-like, smaller than in previous two legs, oöstegite shorter and broader, with two lobes, apically bearing four

slender setae. Segment 2 oblong, hind margin weakly serrate and spinose. Dactyl slender, terminal spine curved.

Peraeopod 6, anterior coxal lobe very shallow, posterior lobe quite deep, expanded posterodistally, hind margin serrate. Gill the largest, sac-like, twisted near the base. Segment 2 ovate, margins spinose, hind margin serrulate. Segment 3 very short, segments 4-6 slender, normally spinose. Dactyl long, slender, terminal spine curved.

Peraeopod 7 the longest, coxal plate fairly shallow, spinulose below. Segment 2 longer than broad, indented above to hinge, expanded in front, serrate behind. Segments 4 to 6 slender, dactyl long, slender, terminal spine curved.

First epimeral plate deep, lower margin oblique, rounded, hind margin convex, serrulate, hind corner sharply obtuse. Second plate broadening distally, lower margin smoothly rounded, posterodistal corner a little produced behind, hind margin slightly sinuous, serrulate. Third plate smaller, subsquare, hind margin almost straight, serrulate, hind corner minutely produced.

First and second pleopods, biramous, inner ramus shorter than outer. Peduncular margins clothed with minute hairs except near the two coupling spines, one plumose seta distally placed on the outer margin of each. Rami generally bearing two long plumose setae on each segment, first pleopod with seven inner and twelve outer ramal segments, second with four inner and ten outer ramal segments. Third pleopod a tiny stump, still with a ramal vestige bearing a terminal spine and a hook-shaped subapical spine. Peduncle pilose on the inner side, with one distal spine and one spine near the outer margin.

Uropod 1, peduncle slender, bearing one inner and two outer marginal spines, apical spine short, strong and curved. Rami slender, subequal, margins of outer ramus naked, those of inner ramus bearing three evenly-spaced spines. Uropod 2 ramus slender, with an inner and two outer marginal spines, rami subequal, outer with naked margins, inner bearing

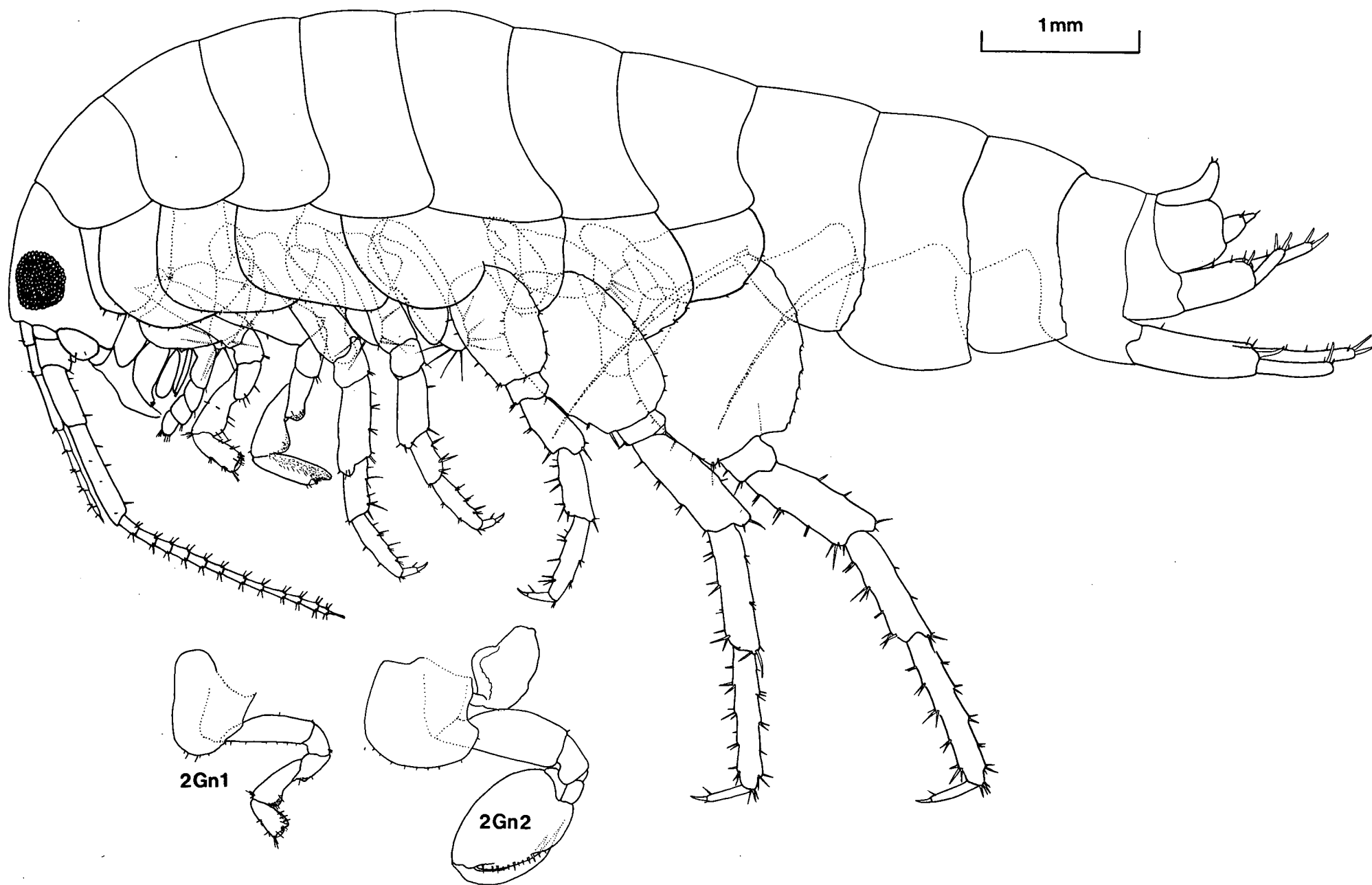


FIGURE 3.12 *Tasmanorchestia annulata* gen. et sp.n., holotype ♀. 2, allotype ♂. Scale a: Mxpd, Mx1&2, UL, LL, Lft Md, Rt Md. Scale b; OP, PD.

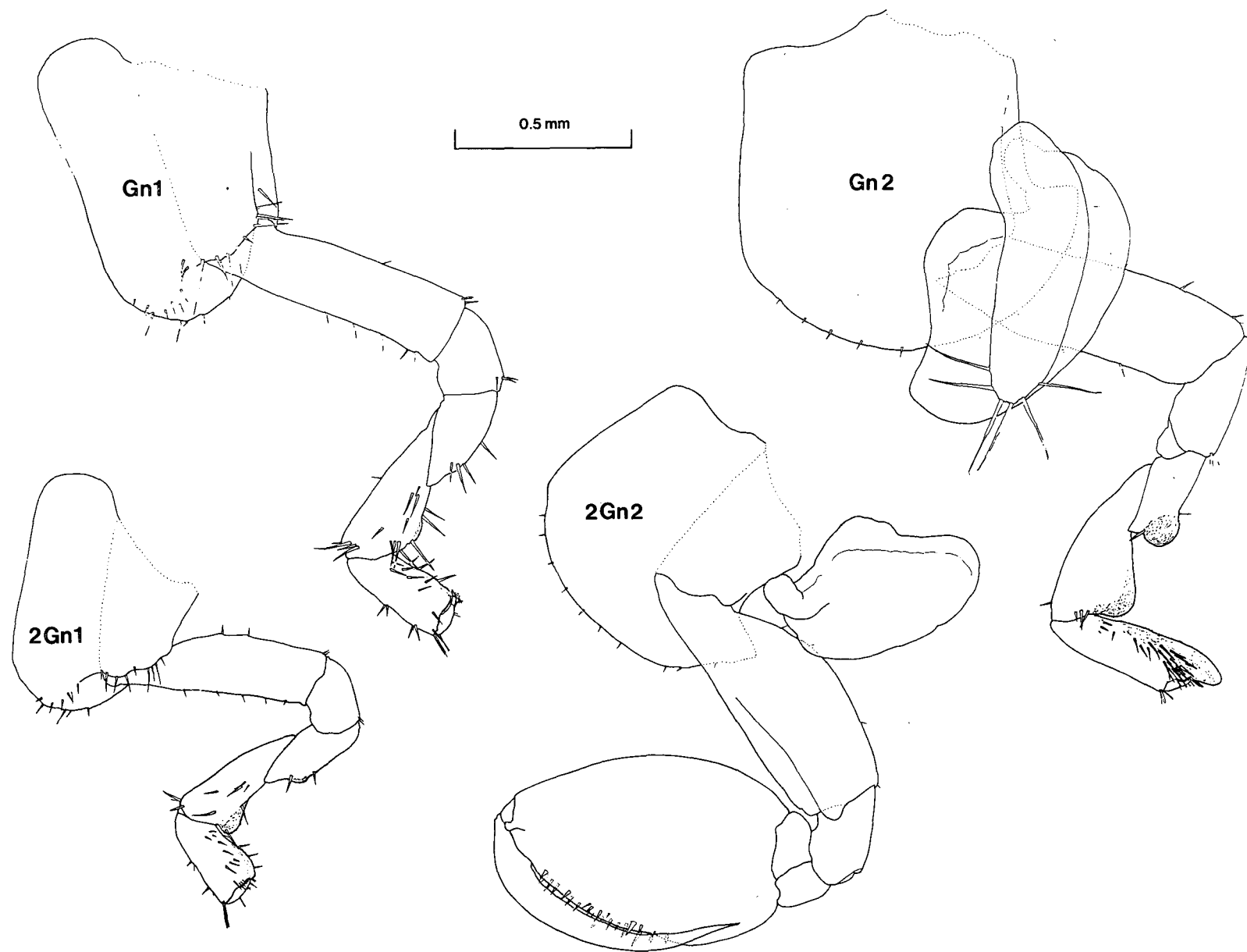


FIGURE 3.13 *Tasmanorchestia annulata* gen. et sp.n., holotype ♀. 2, allotype ♂.

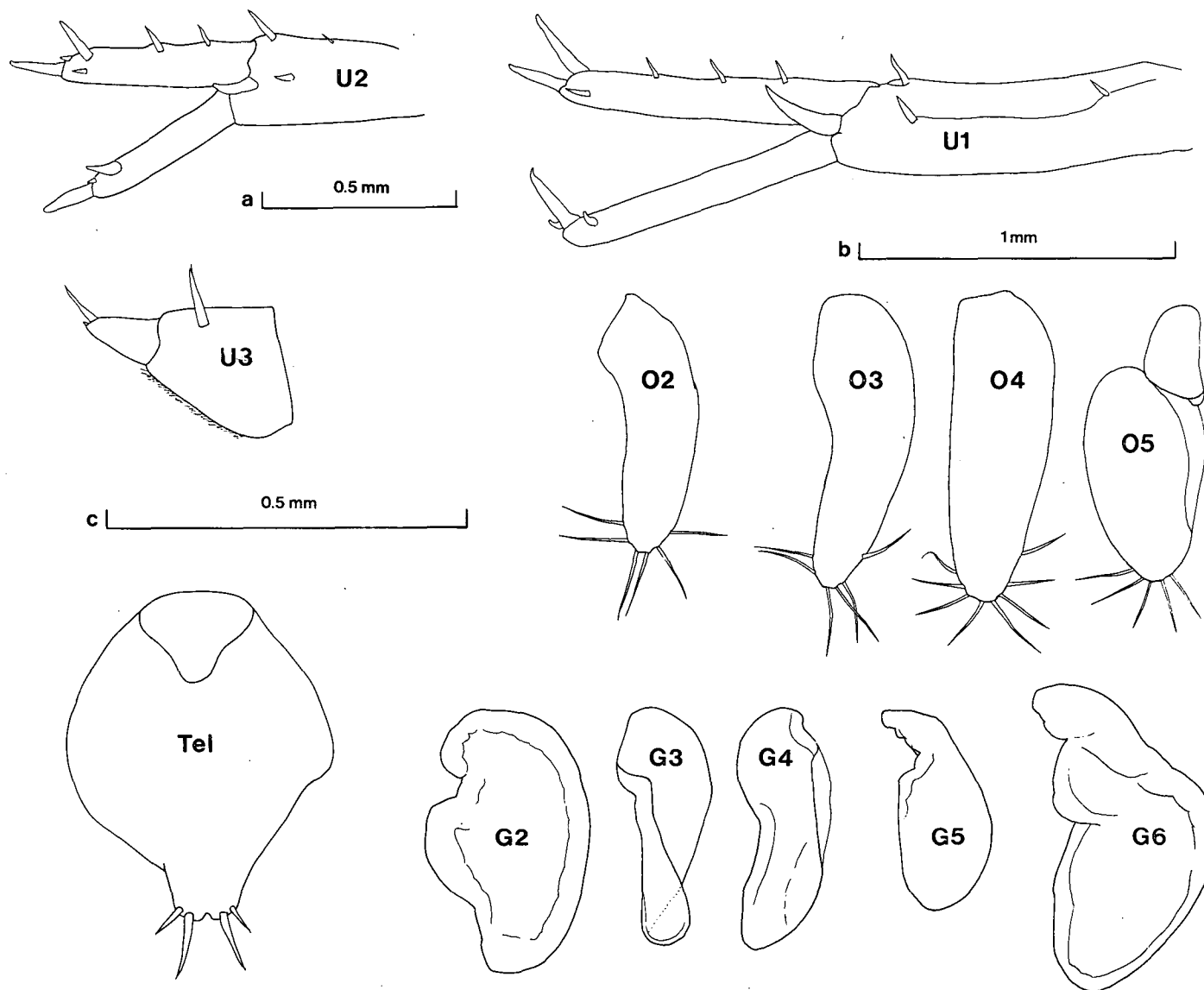


FIGURE 3.14 *Tasmanorchestia annulata* gen. et sp.n., holotype ♀. Scale a; U1&2. Scale b; O2-5, G2-6. Scale c; Tel, U3.

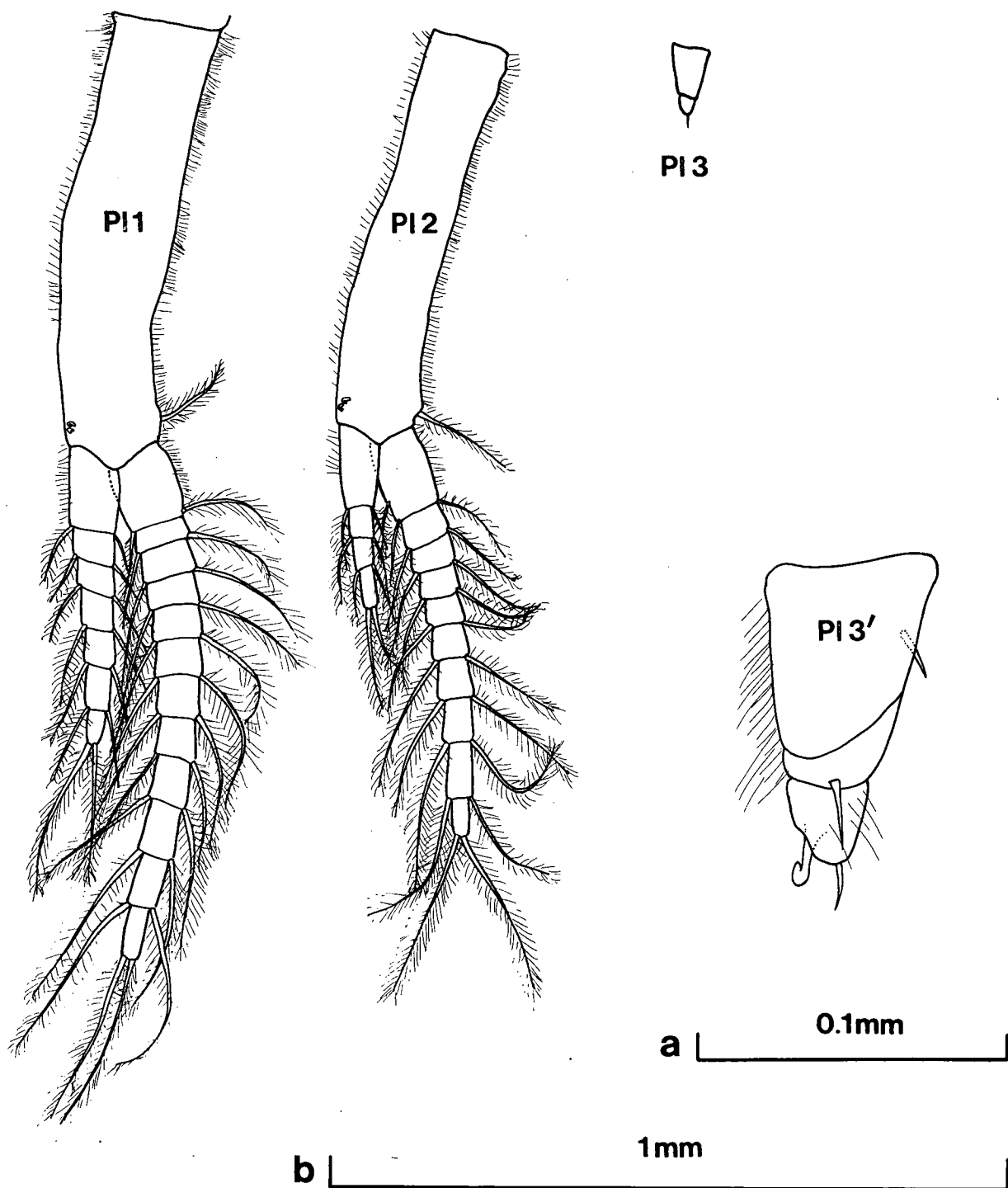


Figure 3.15 *Tasmanorchestia annulata* gen. et sp.n., holotype ♀. P13': enlarged view of P13'. Scale b: P11-3.

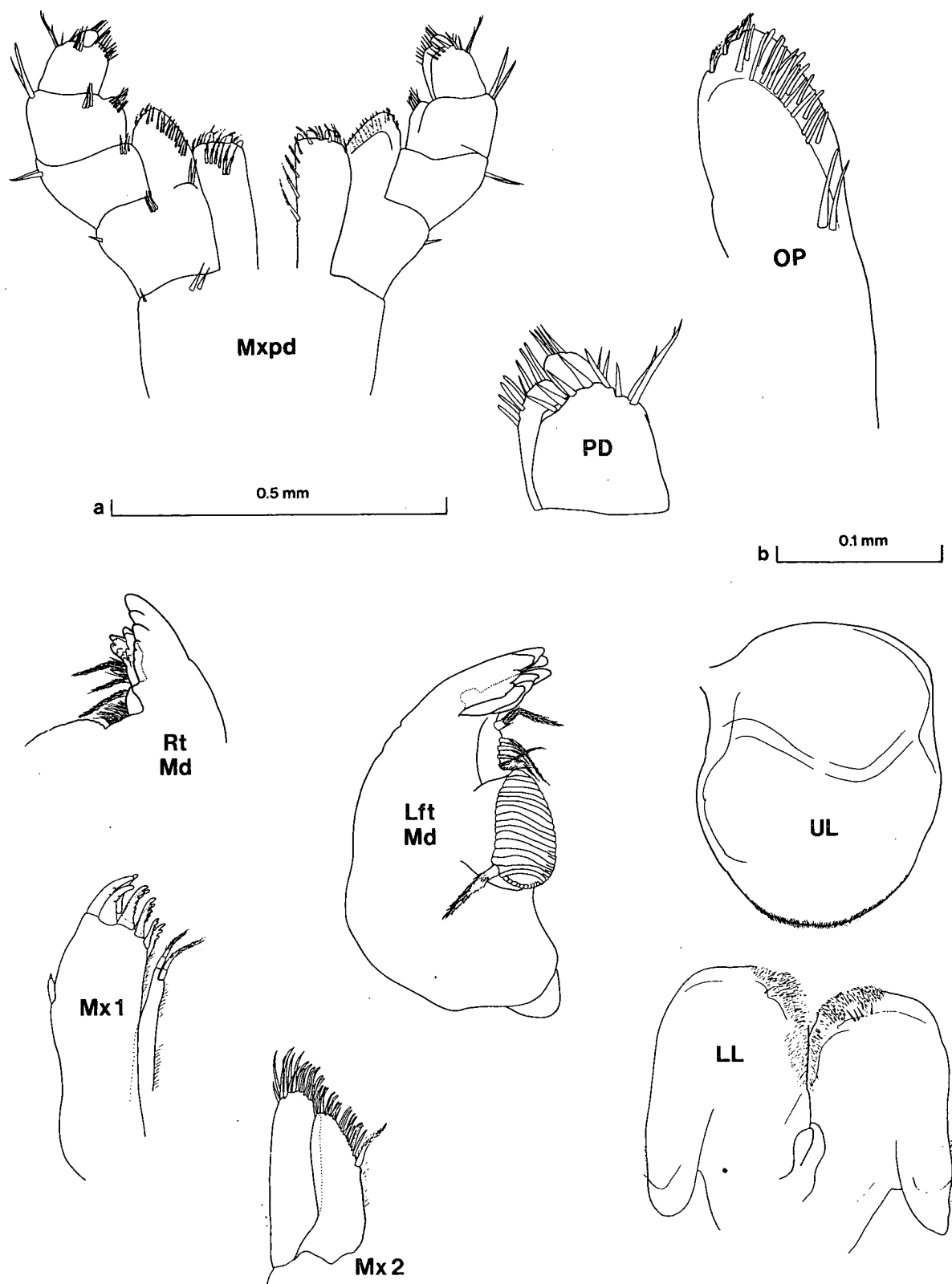


Figure 3.16 *Tasmanorchestia annulata* gen. et sp.n., holotype ♀.
 Scale a: Mxpd, Mx1&2, UL, LL, Lft Md, Rt Md. Scale b:
 OP, PD.

two marginal spines. Uropod 3, peduncle narrowing strongly, lower margin distally straight, pilose, one strong peduncular spine; ramus fairly short, slender, bearing one long and one very short apical spine.

Telson fairly narrow, apex produced, minutely cleft, bearing a long and a short slender apical spine on each side.

Male:

Length 5.6 mm. Antenna 1 flagellum of 4 segments [3-6], flagellum of antenna 2 of 11 segments [5-11].

Gnathopod 1, as in female, but hind margin convex, posterior lobes of segments 4 and 5 more pronounced, so that segment 5 is deep. Segment 6 broadening distally due to posterior tumescence, which also causes palm to exceed dactyl.

Gnathopod 2, coxal plate broad, shallow; posterior process large, acute. Gill sac-like, basally twisted. Segment 2 powerful, hind margin strongly convex, lightly spinulose. Segment 6 large, subovate, palm strongly oblique, convex, lined with small stout spines. Dactyl closely fitting palm, curved, very long, just shorter than segment 6, produced to a long tapering point.

Otherwise like female, but lacking oöstegites and bearing paired ventral penes.

Remarks

This fairly large landhopper has a distinctive laterally striped body (to which the name refers) and is one of three species which are generally found in the vicinity of the coast, especially in the west of Tasmania. Females are significantly larger than males when full grown.

Genus *Neorchestia*, gen. nov.

Diagnosis

Apomorphic, sexually dimorphic landhoppers, maxilliped inner plate sparingly setose, outer plate apically rounded with submarginal spine-row, palp segments 2 and 3 bearing apically spinose, triangular lateral lobes, segment 4 prominent, not masked by segment 3; anterior and posterior gills very large, posterior pair folded and lobate; pleopods reduced, broad, biramous and setose. Also with gnathopod 1 subchelate in both sexes, heavier in ♂, gnathopod 2 minutely chelate in ♀, powerfully subchelate in ♂. Oöstegites slender, terminal setae long, posterior pair broad and thick with gill-like texture. Peraeopods 6 and 7 long, second segments enlarged; uropods 1 and 2 outer rami without marginal spines, uropod 3 small, telson bearing apical spines only.

Type species: *Neorchestia plicibrancha* sp.n.

Remarks

While sexual dimorphism of gnathopods is retained in this genus, a number of apomorphic features are displayed which are usually restricted to the sexually similar group. These include modification of the epimeral plates, strong reduction of the pleopods, a tendency for the rami to lose their segmentation, long, slender second antennae, peraeopods and general body shape, elongate uropod 1 peduncular apical spine, and modified gills, with anterior and posterior pairs greatly enlarged, and the posterior two pairs lobate, lateral lobes of maxilliped palp reduced, and inner plate poorly setose. Perhaps the most striking feature is the gill modification, a fairly common feature amongst apomorphic landhoppers, which apparently facilitates respiration by concentrating gas exchange surfaces at each end of the ventral tunnel formed by the coxal plates

and second segments of peraeopods 5 to 7. This presumably allows more room in the marsupium for the large eggs of terrestrial species. Aquatic species generally have large subequal gills, and those on peraeopods 3 to 5 are pushed down beside the legs; in terrestrial species this would expose these gills to mechanical damage, so a reduction in their size bestows additional advantage.

An undescribed, sexually dimorphic landhopper species is common in southwest Western Australia, with *Austrotroides pectinalis* Friend (in MS, see Appendix). Although the second gnathopods of the males of this species have greatly enlarged, subtriangular propods, the morphology of the maxillipeds, antennae, pleopods and first gnathopods is so similar to that of *N. plicibrancha* sp.n. that these species must be seen as congeneric.

The name of the genus is a contraction of "neo-" and "*Orchestia*", as this group of species possesses both apomorphic features and the basic gnathopod configuration of shore-dwelling *Orchestia* species.

Neorchestia plicibrancha, sp.n.

Figures 3.17 - 3.21

Types

Holotype ♀; 2 km W of Blackhole Lookout, South Coast Track,
S. Tasmania, beside creek. UGR 8210-782722. Coll. JAF, 27.xii.1975
(8210-7). Allotype ♂; same data as holotype. Paratypes 5 ♂♂, 4 ♀♀
(3 ovig.), 3 imm.; same data as holotype.

Other material examined: TASMANIA:

7913-1(2), -2(1)

7914-5(1), -8(2)

7915-14(5), -20(1)

8012-1(1), -3(1), -4(2), -6(10), -7(5), -8(6), -10(2), -11(4),
-12(9), -13(1), -14(5), -15(5), -16(4), -17(9), -18(4), -19(2),
-20(7), -21(4), -22(2), -23(9), -24(6), -26(5), -27(3), -30(5),
-31(10), -32(13), -33(12), -34(4), -41(1), -42(5), -43(5), -44(9),
-46(13), -47(3), -48(3), -50(5), -51(9), -52(2), -53(1), -54(2),
-55(6), -59(2), -61(1), -64(2), -65(1), -66(3), -67(44)

8013-8(5), -10(2), -11(6), -12(8), -14(7), -15(1), -16(13),
-18(7), -19(3), -20(17), -21(1), -22(2), -23(2), -24(8), -25(2),
-33(1), -34(1), -38(4), -39(8), -40(3), -41(11)

8014-2(1), -5(6), -8(2), -9(1), -14(1), -16(2), -17(1)

8110-6(3), -11(1), -12(2), -14(4), -15(4), -23(1), -24(17),

8111-1(10)

8112-5(5), -8(4), -9(2), -10(4), -11(1), 12(2), -13(4), -15(64),
-16(2), -17(10), -19(2)

8113-4(1), -5(3), -6(17), -7(3), -8(8), -10(24), -11(10), -12(16),
-13(2)

8210-3(6), -5(3), -8(7), -10(13), -15(2), -16(4), -18(1)

8211-1(10), -2(11), -5(5), -6(19), -7(2), -8(4), -9(3),
 -11(10), -12(3), -13(2), -14(1), -15(3), -16(1), -17(3),
 -19(3), -25(1), -30(2)
 8212-5(1), -6(1), -7(1), -8(14)

Diagnosis

A sexually dimorphic landhopper with slender appendages, enlarged, complex anterior and posterior gills and reduced but biramous plumose pleopods.

Description

Female:

Length 8.8 mm, bearing no eggs [2-4]. Head deeper than long, eye almost round, large, width more than one-third head length. Antenna 1 exceeding midpoint of last peduncular segment of antenna 2, flagellum of six segments [3-6], shorter than peduncle. Antenna 2 as long as head and first five pereon segments, last peduncular segment slender, shorter than rest of peduncle; flagellum longer than peduncle, 17-segmented [7-20], most segments bearing 4 groups of 3 long slender setae, longer than the width of each segment.

Upper lip deep, distally finely pilose, indentation of right margin prominent. Lower lip fairly deep, lateral lobes large, pilosity of inner shoulders not extending into proximal area of central cleft. Left mandible with 4 cusps, lacinia mobilis 5-cusate, molar with 15 striations. Right mandible 5-cusate, lacinia 3-dentate. Maxilla 1, inner plate long, apical plumose setae strong; outer plate fairly slender, not narrowing distally; palp 2-segmented, distal of midpoint of outer margin; apical spines long, strong and dentate, mostly longitudinally set, dentition formula 2-1-3-4-4-4-4-4-5. Maxilla 2 inner plate slender, much narrower but just shorter than outer plate, apical spines short, round-tipped

at outer end, longer and sharper near the long plumose seta. Outer plate broad, narrowing distally, four small spines and a plumose seta near outer apical margin, five or six long sharp distally serrate spines near the apex, row of spines on inner distal margin strong, spines curved, blunt ended.

Maxilliped inner plate apically truncate, bearing three unequal spine-teeth and several plumes on the apex, five plumose spines on the lateral face, on the medial face two near the inner margin and three subapically. Outer plate distally rounded, submarginal spine-row strong, spines stout and blunt-tipped. Palp fairly broad, lateral lobes of segments 2 and 3 distinct but each reduced to a triangular projection capped by a strong group of spines; medial spines of segment 3 small, slender; fourth segment prominent, relatively large, apically rounded and bearing 5-6 blunt spines.

Gnathopod 1, coxal plate broad, shallow anterodistal corner sharp, lower margin bearing a few slender spines. Segment 2 sublinear, with several spines on each margin. Segment 4 with a shallow posterior lobe, segment 5 long and deep, bearing several long medial spines and a strong tumescence behind; segment 6 shorter, hind margin convex, distally almost square, short palm defined by group of spines near rounded posterodistal corner, equalled by dactyl.

Gnathopod 2, coxal plate broad, rounded below, posterior process large. Gill very large, with a long, broad anterior extension; oöstegite slender, much shorter than segment 2, bearing five long, slender setae near the rounded apex. Segment 2 strong, expanded anteriorly, segment 3 equal to 4 which bears a strong tumid lobe. Segment 5 deep, poorly spinose, hind lobe deep and broad. Segment 6 just longer, slightly broadening distally, hind margin convex, apical lobe strong; medial spine row composed of small spines, lateral row of long slender spines. Dactyl oblique.

Peraeopod 3, coxal plate shallow, lower margin sparsely spinose,

posterior process prominent. Gill small with a distal anterior projection; oöstegite small, slender, with eight distal setae. Segment 2 strong, slightly curved anteriorly, segments 4-6 slender, dactyl small.

Peraeopod 4 similar to 3, but coxal plate shallower and posterior process more blunt-ended, segments 2 and 4-6 shorter.

Peraeopod 5, anterior coxal lobe shallow, with a few spines below, posterior lobe just shorter, rounded behind. Gill fairly large, folded in half with a slender papillate distal lobe, oöstegite almost as long as that of gnathopod 2, but broader and thicker than the others, texture resembling a gill, apically bearing three tiny spines. Segment 2 subovate, spinose and convex behind. Segments 4-6 slender, bearing long spines. Dactyl slender, terminal spine almost straight.

Peraeopod 6 long, anterior coxal lobe very shallow, posterior lobe deep, expanded posterodistally giving it an oblique orientation. Gill large, complex, formed of several lobate folds and a posterior papillate lobe. Segment 2, large, subovate, spinose behind and expanded to form a shallow distal lobe. Segments 4-6 bearing long spines, 6 very slender. Dactyl long, slender, terminal spine almost straight.

Peraeopod 7 just longer than 6, coxal plate shallow, spinulose behind. Segment 2 very large, serrulate hind margin expanded below forming a distal lobe. Segments 4-6 bearing long spines, segment 6 very slender. Dactyl long, slender.

First epimeral plate shallow, rounded below, posterodistal corner sharp, hind margin convex, spinulose. Second plate projecting well below third, front and lower margins forming a single smooth curve, hind corner obtuse, just rounded, hind margin gently convex, spinulose. Third epimeral plate subsquare, hind corner sharply rounded, hind margin straight, spinulose.

Pleopods all reduced but biramous and setose, progressively shorter and peduncles broader posteriorly; inner rami shorter than outer

rami, all peduncles bearing two coupling spines. First pleopod, peduncle longer than rami, second pleopod, peduncle subequal to longer ramus, third pleopod, peduncle shorter than longer ramus. Segmentation of rami indistinct, but inner and outer ramal segment numbers 5 and 7, 3 and 7, 3 and 6 on first, second and third pleopods respectively. All rami bearing fairly short plumose setae on margins, peduncles naked.

Uropod 1, peduncle bearing four inner and six outer marginal spines, apical spine slender, curved and very long, half the length of the rami; outer ramus subequal to inner, margins naked but with a minutely serrulate patch proximally on the upper margin, inner ramus armed with three marginal spines. Uropod 2, peduncle bearing two inner and four outer spines; rami just shorter, subequal, outer ramus bearing no marginal spines but minutely serrulate along the upper margin, inner ramus with two marginal spines; one apical spine on each ramus very long, almost half as long as ramus. Uropod 3 peduncle short, broad, with a very long spine and a shorter spine near the midpoint of the upper margin, ramus slender, small, apically bearing two unequal spines.

Telson broad, apex almost a right angle, minutely cleft, with an apical spine on each side.

Male:

Length 8.1 mm. Antenna 1, flagellum of five segments [3-6], flagellum of antenna 2 with 18 segments [7-20].

Gnathopod 1, like that of ♀ but posterior lobe of segment 5 deeper, segment 6 broadening distally due to posterior tumid lobe, which projects distally past tip of closed dactyl; palm thus exceeds slender dactyl.

Gnathopod 2, coxal plate similar to that of ♀ but gill smaller; segment 2 strong, expanded posteriorly, anterior trough present on medial side into which powerful subchelate hand folds; segment 6 subovate, large, palm oblique, lined with short, stout spines, dactyl strong, curved and

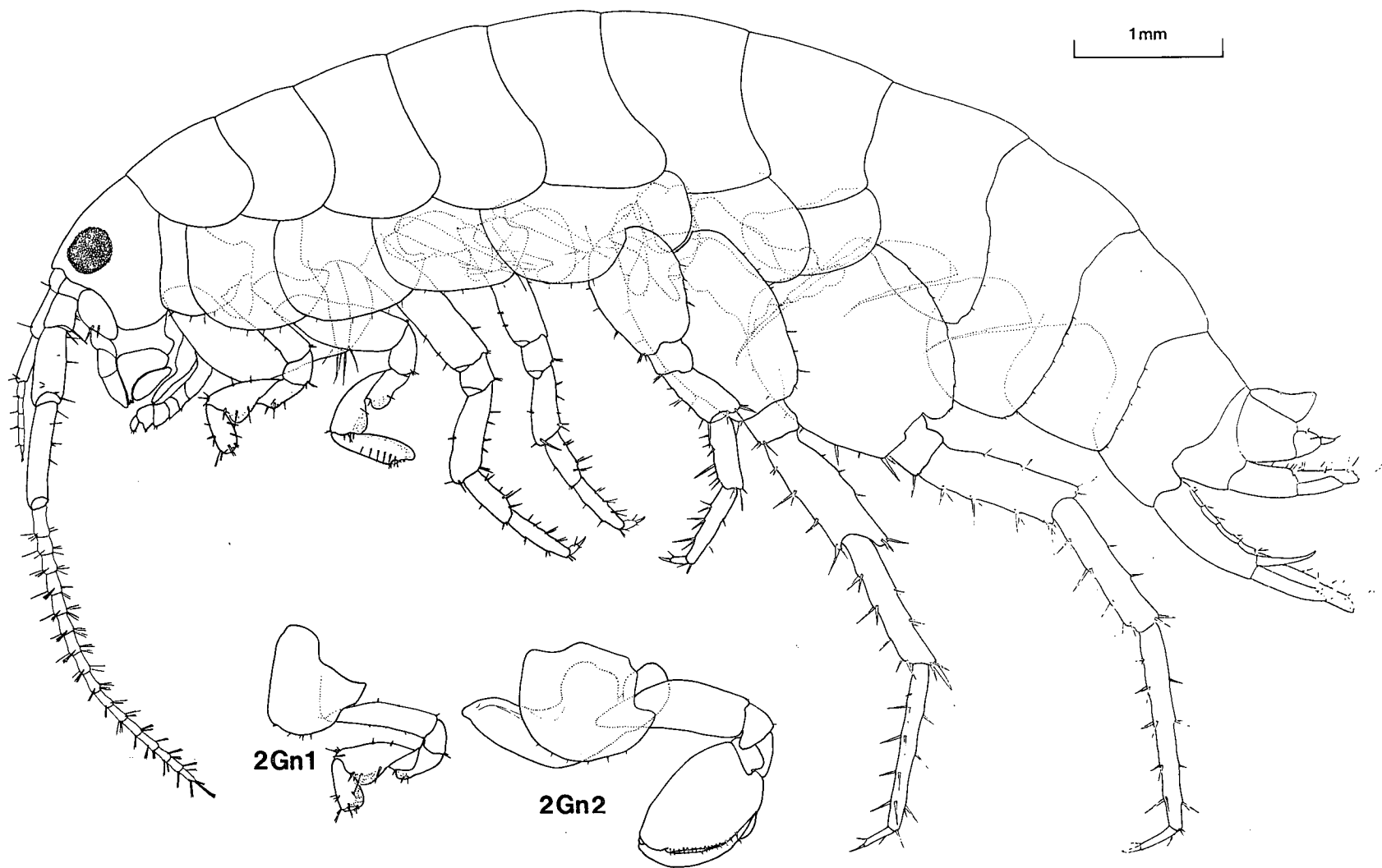


FIGURE 3.17 *Neorchestia plicibrancha* gen. et sp.n., holotype ♀. 2, allotype ♂.

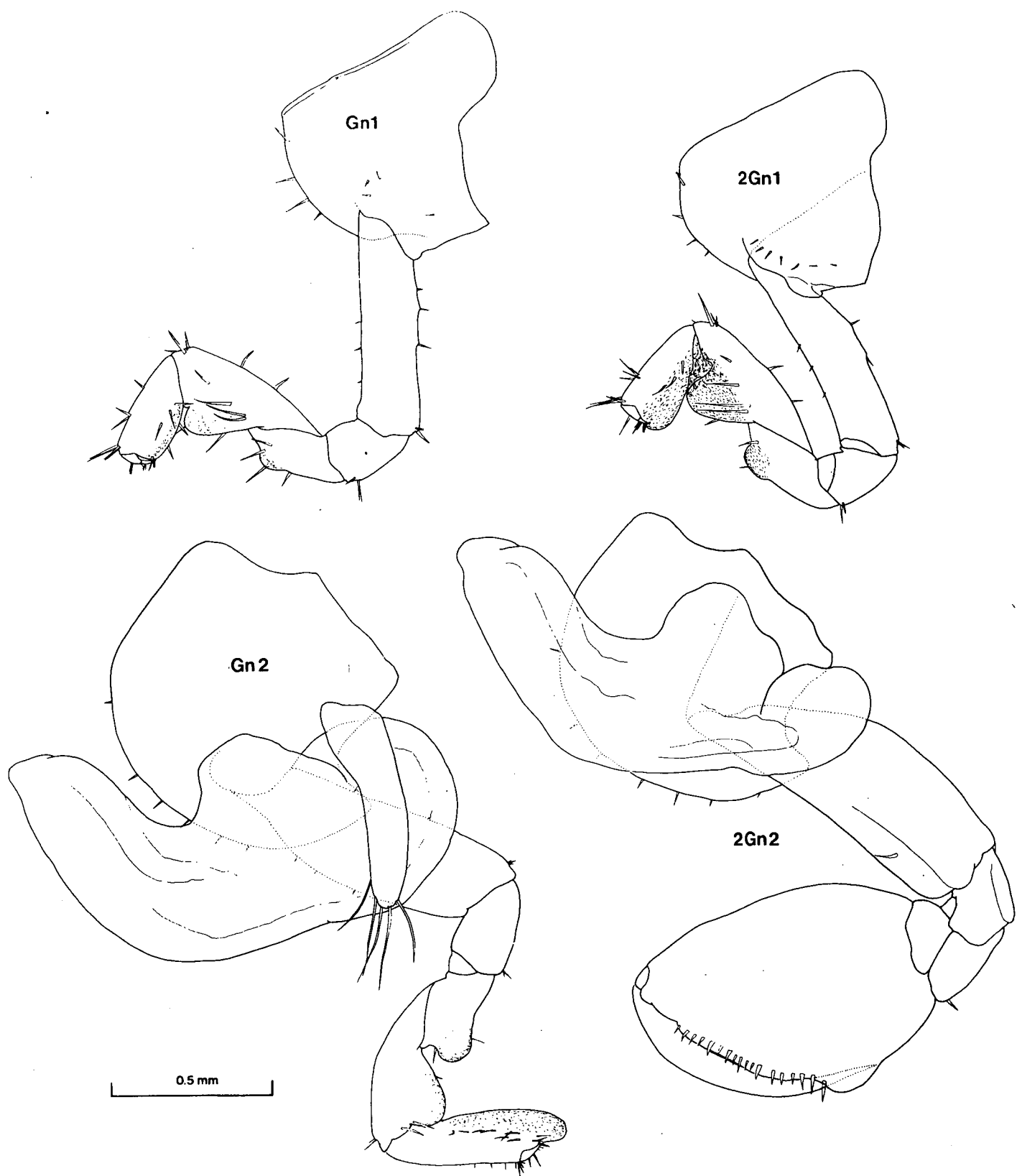


FIGURE 3.18 *Neorchestia plicibrancha* gen. et sp.n., holotype ♀. 2, allotype ♂.

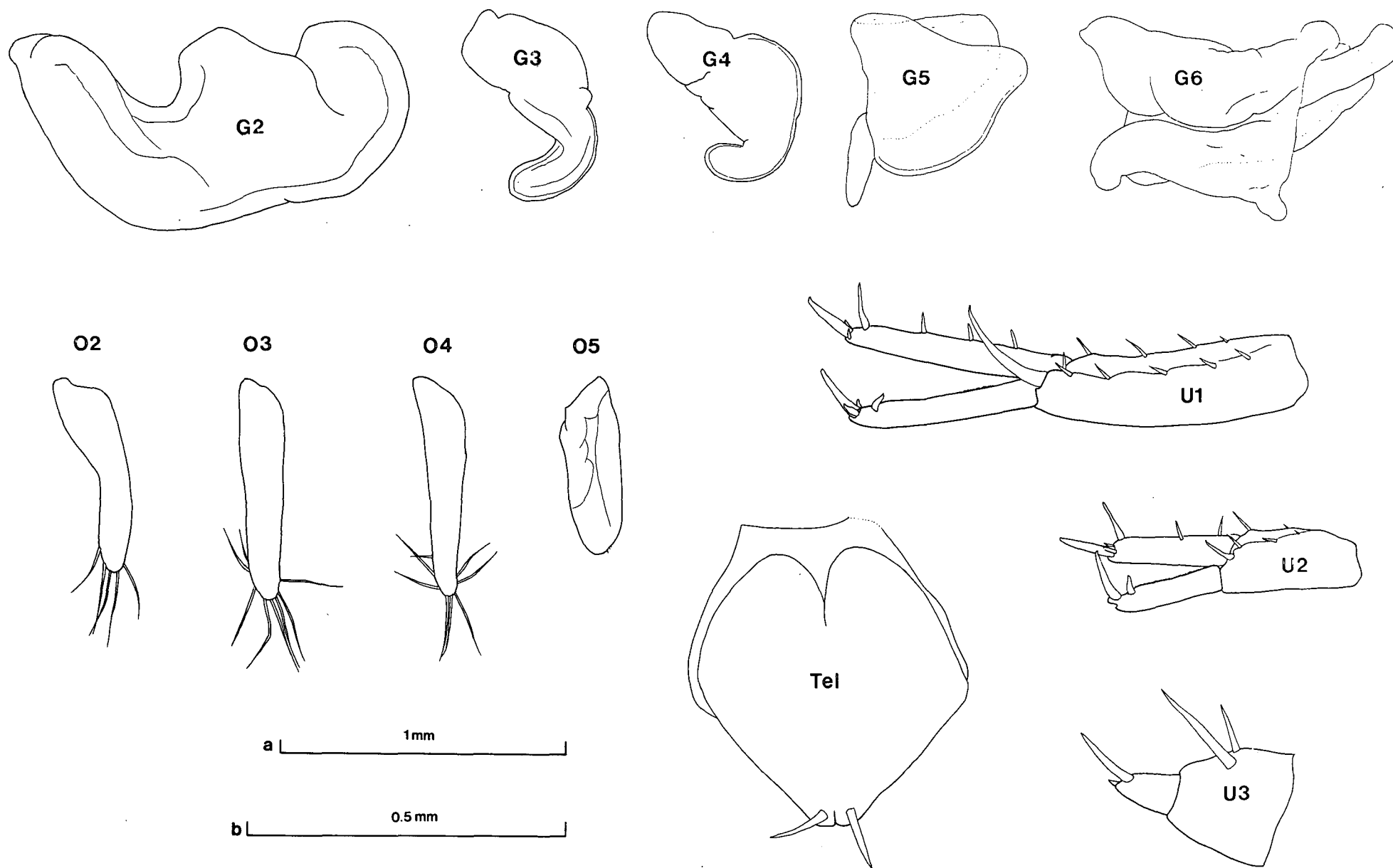


FIGURE 3.19 *Neorchestia plicibrancha* gen. et sp.n., holotype ♀. Scale a; G2-6, O2-5, U1&2.
Scale b; Tel, U3.

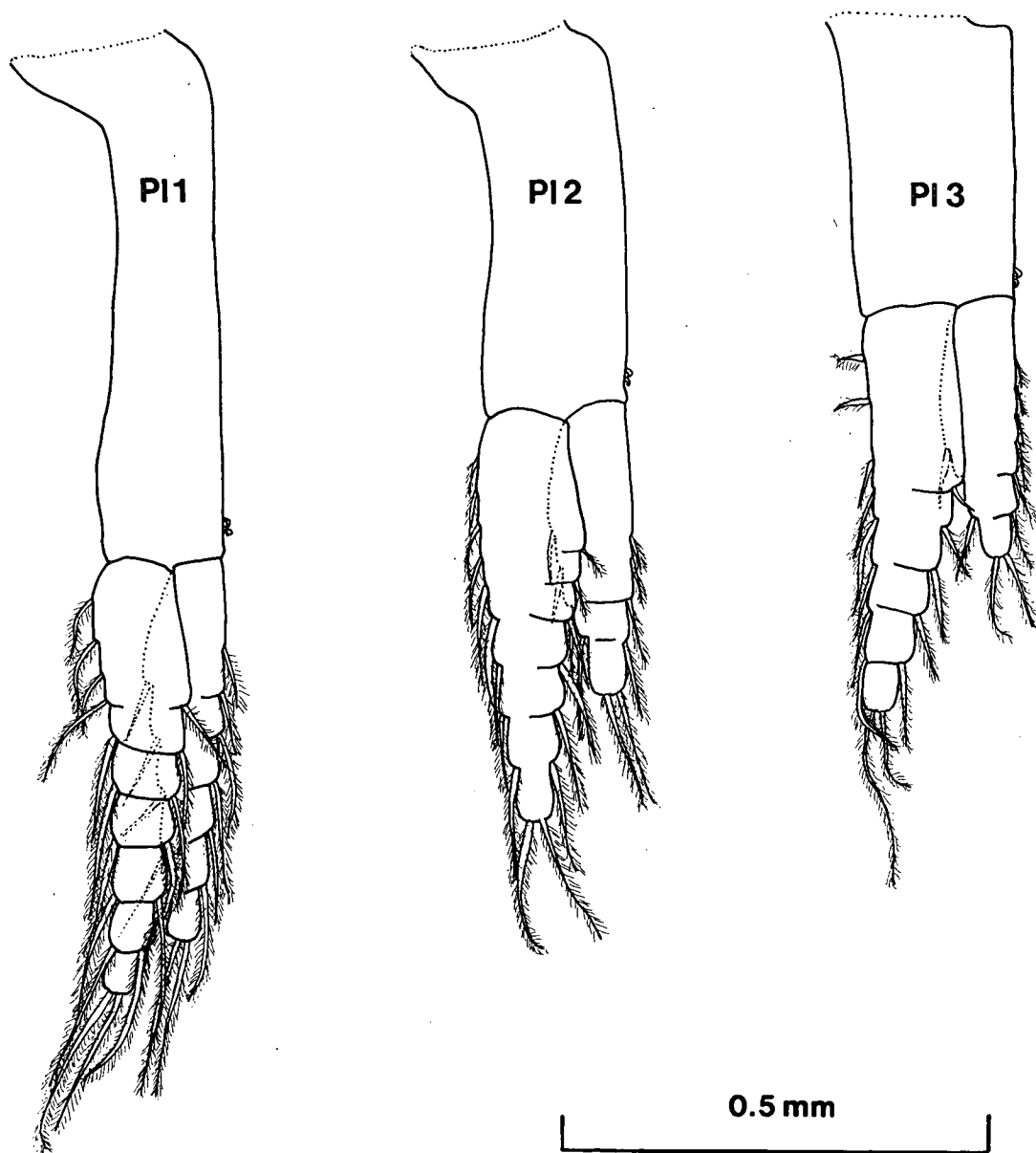


FIGURE 3.20 *Neorchestia plicibrancha* gen. et sp.n., holotype ♀.

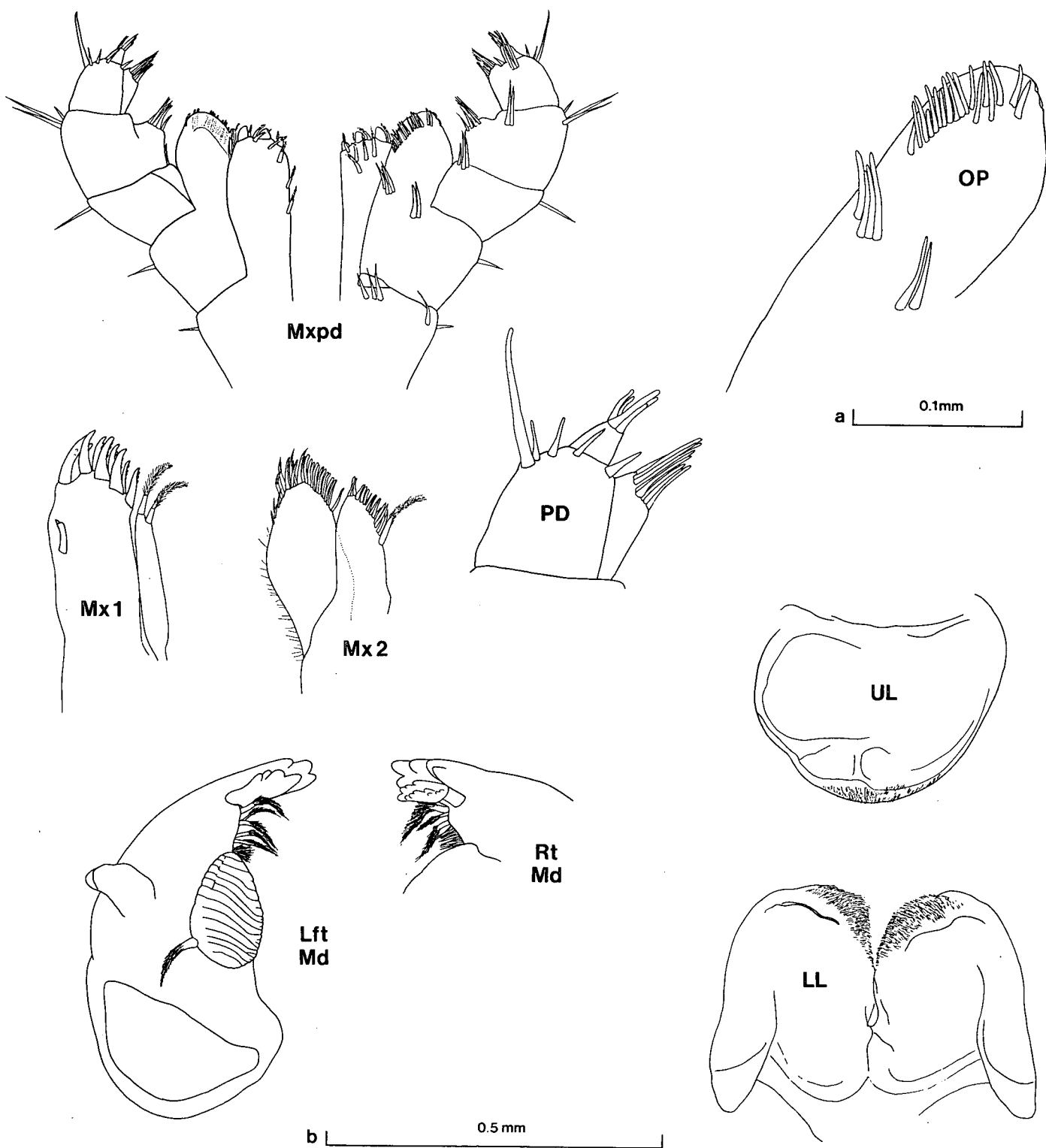


FIGURE 3.21 *Neorchestia plicibrancha* gen. et sp.n., holotype ♀. Scale a; OP, PD. Scale b; Mxpd, Mx1&2, Lft Md, Rt Md, UL, LL.

sharp distally, closing between a pair of spines against a flange-like projection at the proximal end of the palm.

Otherwise similar to ♀ but lacking oöstegites and bearing paired ventral penes.

Remarks

N. plicibrancha sp.n. is widespread in western Tasmania (see Chapter 4). This is seen as evidence of its successful adaptation to the terrestrial environment in a high-rainfall area.

Live specimens are distinguished from other species by their extremely agile hopping. Adult males and females are of similar size. The specific epithet means "with folded gills".

Genus *Austrotroides*, Friend MS

Austrotroides Friend in MS (see Appendix)

Diagnosis

Sexually similar landhoppers with slender appendages. Antennae long, first exceeding midpoint of last peduncular segment of second. Maxilliped outer plate apically rounded or bluntly produced, submarginal row of spines present, although sometimes clustered near apex. Palp segments 2 and 3 bearing spinose lateral lobes; segment 4 distinct, small, masked by lateral lobe of segment 3. Gnathopod 1 strong, segment 6 with a very small palm only, or secondarily swollen in both sexes; segment 6 of gnathopod 2 long, slender and mitten-shaped. Anterior and posterior gills well developed; gnathopod 2 gills large, peraeopod 6 gills large, somewhat lobate proximally. Other gills smaller, those of peraeopods 3 and 4 basically sac-like, peraeopod 5 gill bilobate. Four pairs of oöstegites present, anterior three long, apical setae short, posterior pair somewhat reduced. Epimeral plate 1 deep, plates 2 and 3 slightly produced behind, convexly rounded below. Pleopods reduced or vestigial, rami short or absent. Uropods 1 and 2 long, slender, outer ramus of uropod 2 not shorter than inner; outer ramus of first pair lacking marginal spines, peduncular apex with a long curved simple spine. Telson apically with a small cleft.

Type species: *Austrotroides pectinalis* Friend (in MS)

Distribution: Western Australia

Other species: *A. occidentalis* Friend (in MS)

Distribution: Western Australia

A. crenatus Friend (in MS)

Distribution: South Australia

A. longicornis sp.n.

A. leptomerus sp.n.

A. maritimus sp.n.

Remarks

This genus displays a combination of plesiomorphic and apomorphic features. The following characteristics of the genus are generally found in the more plesiomorphic, sexually dimorphic species:

broad spinose maxilliped palps with the fourth segment entirely masked, rounded outer plate with numerous blunt submarginal spines, setose inner plate with small apical spine-teeth;

deep, narrow upper and lower lips, maxillae 1 and 2;

broad oöstegites bearing lateral as well as apical spines;

gnathopod 1, inner shelf present, though weak;

elongate uropod 3 ramus with lateral spines; apically cleft telson.

However, *Austrotroides* also shows a number of features otherwise found in more advanced groups of landhoppers:

reduced, usually vestigial pleopods;

long, slender peraeopods;

slender gnathopods, similar in both sexes;

enlarged anterior and posterior gills, last pair long and anseriform (like the head, neck and upper body of a goose, in lateral view).

Three species of *Austrotroides* are found in mainland Australia (Friend, in MS, see Appendix). The Tasmanian species share several features not found in the northern species, although these differences are not sufficiently great to warrant further generic division. In the Tasmanian species the maxilliped outer plate spines form a submarginal row rather than a subapical group, gnathopod 2 gill has a slender anterior extension rather than a broad, rounded one, and segment 2 of peraeopod 7 is narrowly expanded behind, the hind margin distally indented and not forming the distinct distal lobe found in the mainland species. No

mainland species of *Austrotroides* has spines on the outer ramus of uropod 2 (as do two of the Tasmanian species) and all three Tasmanian species have vestigial pleopods (those of *A. occidentalis* are biramous and setose).

Austrotroides longicornis, sp.n.

Figures 3.22 - 3.25

Types:

Holotype ♀ (ovig., 2 eggs); Left bank of South Cape Rivulet, South Coast Track, S. Tasmania. In rotten eucalypt wood, above ground. UGR 8210-826726 Coll. PA, 6.ix.1976 (8210-4). Allotype ♂; 200 m S. of Catamaran R., inland side of Cockle Ck. Rd., under a large *E. obliqua* UGR 8210-907793 Coll. JAF, 23.viii.1974 (8210-1). Paratypes ♂, 2 ♀♀; same data as allotype.

Other material examined: TASMANIA:

8112-12(1)

8210-4(7), -6(2), -8(1), -9(3)

8211-2(1), -9(1), -23(1), -27(1)

8411-4(3), -5(1)

Diagnosis

A large, slender-bodied landhopper, with very long, slender antennae, peraeopods and uropods, sexually similar gnathopods, pleopods reduced to vestigial stumps.

Description

Female:

Length 14.2 mm, ovigerous, with 2 eggs [2-9]. Head longer than deep, eye almost round, width just over one quarter head length. Antenna 1 very long, reaching three-quarters along last peduncular segment of antenna 2; flagellum of eight segments [most found; 9], longer than peduncle. Antenna 2 also long and slender, as long as head and first five peraeon segments, peduncular segment 5 long, slender, longer than rest of peduncle; flagellum much longer than peduncle, of 29 long segments [most found; 30] mostly bearing four groups of 3 bristles longer than the

width of the segment.

Upper lip deep, apically pilose, indentation of right distal margin quite prominent. Lower lip narrow, inner shoulders thickly pilose, margins of central trough lightly pilose, naked proximally. Left mandible 5-cusate, lacinia mobilis with 5 teeth, molar 21-striate. Right mandible 5-cusate, lacinia bicusate with proximal ridge crenulate. Maxilla 1 inner plate short, terminal plumose setae quite long; outer plate narrowing distally, stout 2-segmented palp at broadest part, terminal spines short, dentition formula 1-3-0-5-5-4-4-5-6. Maxilla 2, plates slender, inner shorter and narrower, apical spines short, densely set, longer at inner end of distal margin, proximal plumose seta slender. Outer plate bearing two long sharp apical spines, distal spine row of short uneven spines.

Maxilliped inner plate narrow, broadening distally, apical spine-teeth prominent, outer largest, inner smallest; seven plumose setae on inner margin, four submarginal on medial surface, eight grouped subapically on lateral surface. Outer plate quite broad, apex obtusely rounded, strong submarginal spine-row with blunt spines grouped in pairs. Palp fairly broad, spines on lateral surface quite small, substantial lateral lobes on second and third segments; medial face of lobe on second segments crenulate, inner margin well spined, lobe on third segment broad, spinose, masking small fourth segment which carries several apical spinules.

Gnathopod 1, coxal plate rounded below, inner shelf weak with a few long spines, segment 2 long, slender, broadening distally, anterior margin spinose. Segment 4 spinose behind, tumescence hardly discernible. Segment 5 longer than 6, deep, posterior tumescence deep and long, surrounded by numerous spines on lateral and medial sides. Segment 6 long, almost linear, narrowing slightly distally, with a short oblique palm defined by a small posterior spine-group; posterior margin quite densely spinose, anterior margin with three small groups of spines. Dactyl strong, exceeding palm, terminal spine curved.

Gnathopod 2, coxal plate deep, lower margin smoothly rounded, spinulose, posterior process prominent, acute. Gill large, distal part broad, anterior extension a small slender lobe; oöstegite broad, bearing thirteen slender setae near apex and along distal half of anterior margin. Segment 2 long, broadening gently distally, anterior margin spinose. Segment 4 very weakly spinose, posterior tumescence prominent. Segment 5 very elongate, slender, posterior margin expanded into a broad lobe, a row of spines present near the distal margin. Segment 6 shorter but also slender and elongate, terminal lobe prominent, medial spine-row composed of tiny spinules. Dactyl small.

Peraeopod 3, coxal plate broader than deep, smoothly rounded below, spinulose; posterior process acutely rounded. Gill simple, sac-like, oöstegite fairly broad, just shorter than segment 2, bearing thirteen setae around apex and along distal half of anterior margin. Remainder of limb long, slender, segment 6 spinose behind, dactyl slender, terminal spine long.

Peraeopod 4, coxal plate like 3 but posterior process smaller, blunt-ended; oöstegite with twelve setae, more distally placed; limb otherwise similar to peraeopod 3.

Peraeopod 5, anterior coxal lobe broad, smoothly rounded below, lightly spinulose; posterior lobe small, much shallower, almost straight behind. Gill small, bilobed; oöstegite about two-thirds as long as the others, bearing three slender setae and two spinules near the apex. Segment 2 small, narrowing evenly distally, hind margin almost straight, spinulose. Segments 4-6 long, slender, spinose, dactyl slender, terminal spine quite long.

Peraeopod 6, posterior coxal lobe semi-circular below, posterodistally serrulate. Gill large, distally lobate, anseriform, with posterior constriction just before distal "head" section, which tapers to a rounded apex. Segment 2 slender-ovate, hind margin convex and serrulate, distal lobe present, small. Segments 4-6 elongate, slender, bearing many groups

of fairly small spines. Dactyl slender, terminal spine almost straight.

Peraeopod 7, coxal plate small, serrulate posterodistally. Segment 2 broad-ovate, hind margin serrate, spinulose, meeting trunk of segment some distance from its distal end. Segments 4-6 extremely elongate, slender and well spined; segment 6 bearing 9 groups of spines on the anterior margin. Dactyl elongate, slender, terminal spine slightly curved.

First epimeral plate deep, lower margin oblique, rounded posteriorly; hind margin convex and serrulate. Second plate larger than third, anterior corners smoothly rounding, lower margins convex, hind corners sharp, almost square; hind margins fairly straight, distally serrulate.

Pleopods all reduced to peduncular vestiges; first as long as depth of seventh coxal plate, naked peduncle narrowing from base to near midway, apex rounded. Second pleopod a tiny stump less than one-third as long as first, narrowing distally, with a small submarginal spine. Third pleopod an even smaller stump, bearing one spine and some marginal pilosity.

Uropod 1 elongate, peduncle slender, bearing inner and outer marginal rows of six spines and a curved apical spine; rami slender and long, subequal, shorter than peduncle; outer ramus without marginal spines, armed distally with four strong spines, one as long as the peduncular apical spine, the other three smaller; inner ramus with six small marginal spines, two large and two small distal spines. Uropod 2 also elongate, peduncle poorly spined, slender and just longer than the subequal rami, both of which bear three marginal spines. Uropod 3 long, peduncle sub-cylindrical, bearing one slender spine; ramus slender, elongate, with two marginal spines and two unequal apical spines.

Telson broad, apically minutely cleft, bearing a tiny spine on each apical lobe.

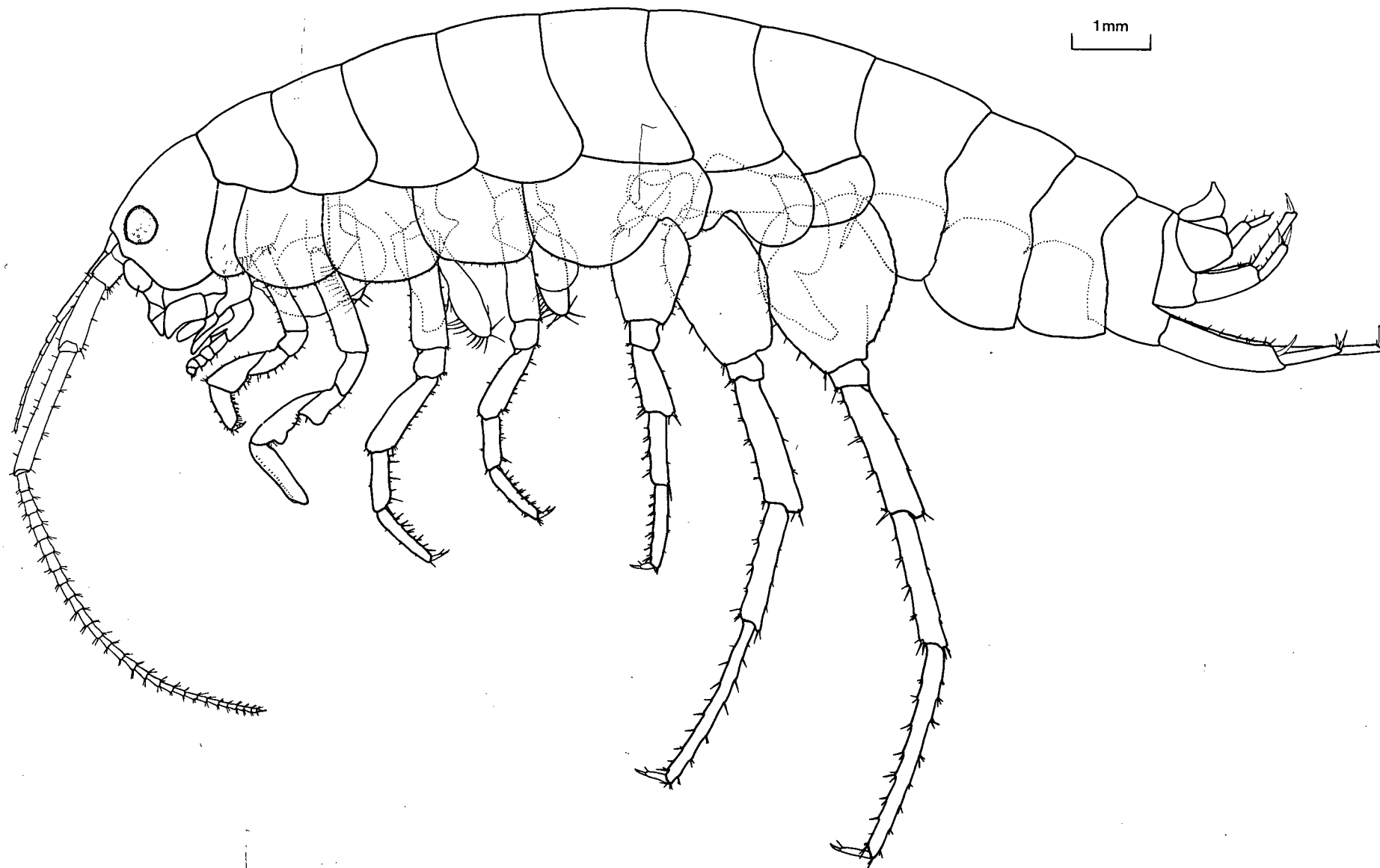


FIGURE 3.22 *Austrotroides longicornis* sp.n., holotype ♀.

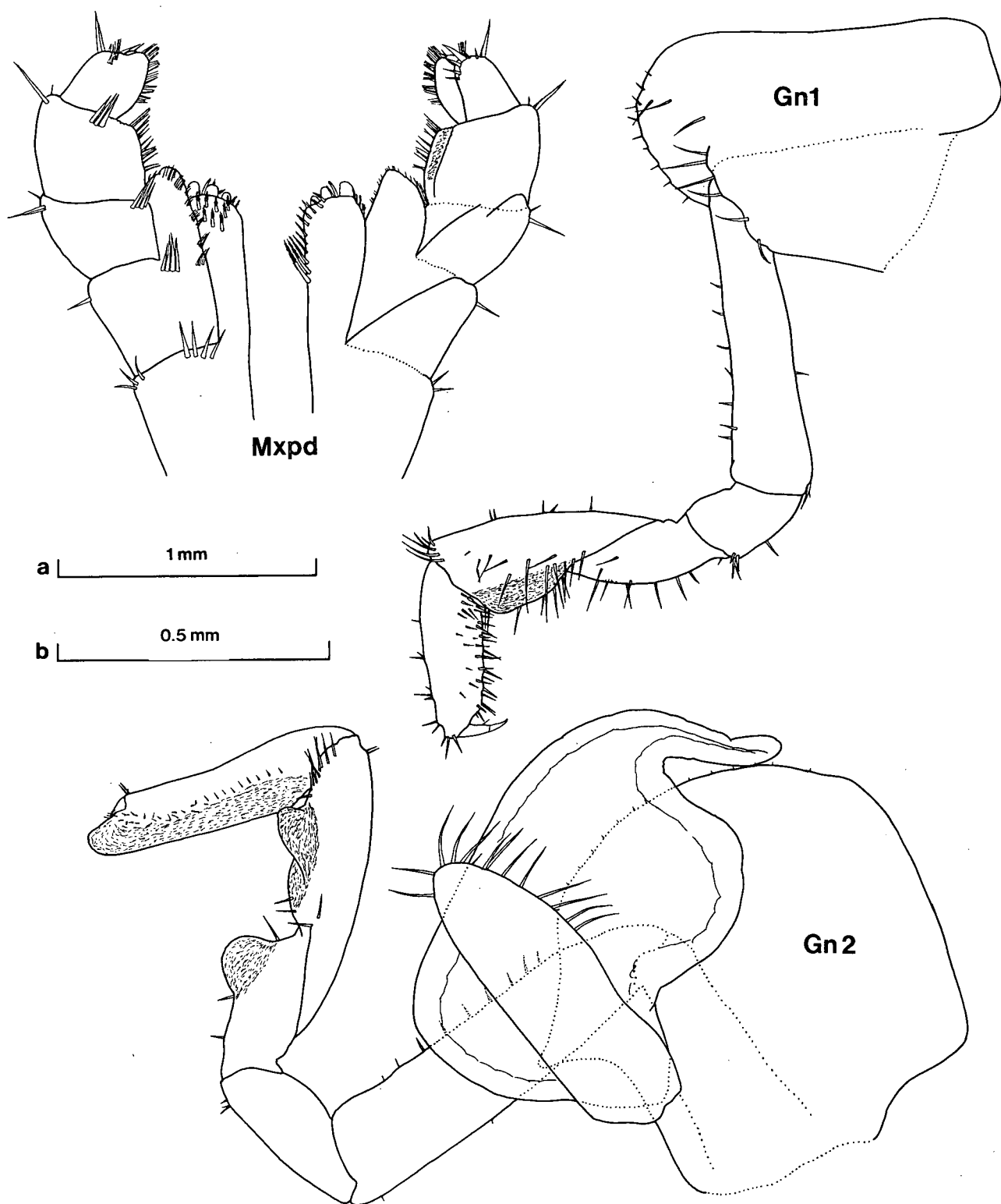


FIGURE 3.23 *Austrotroides longicornis* sp.n., holotype ♀. Scale a; Gn1&2. Scale b; Mxpd.

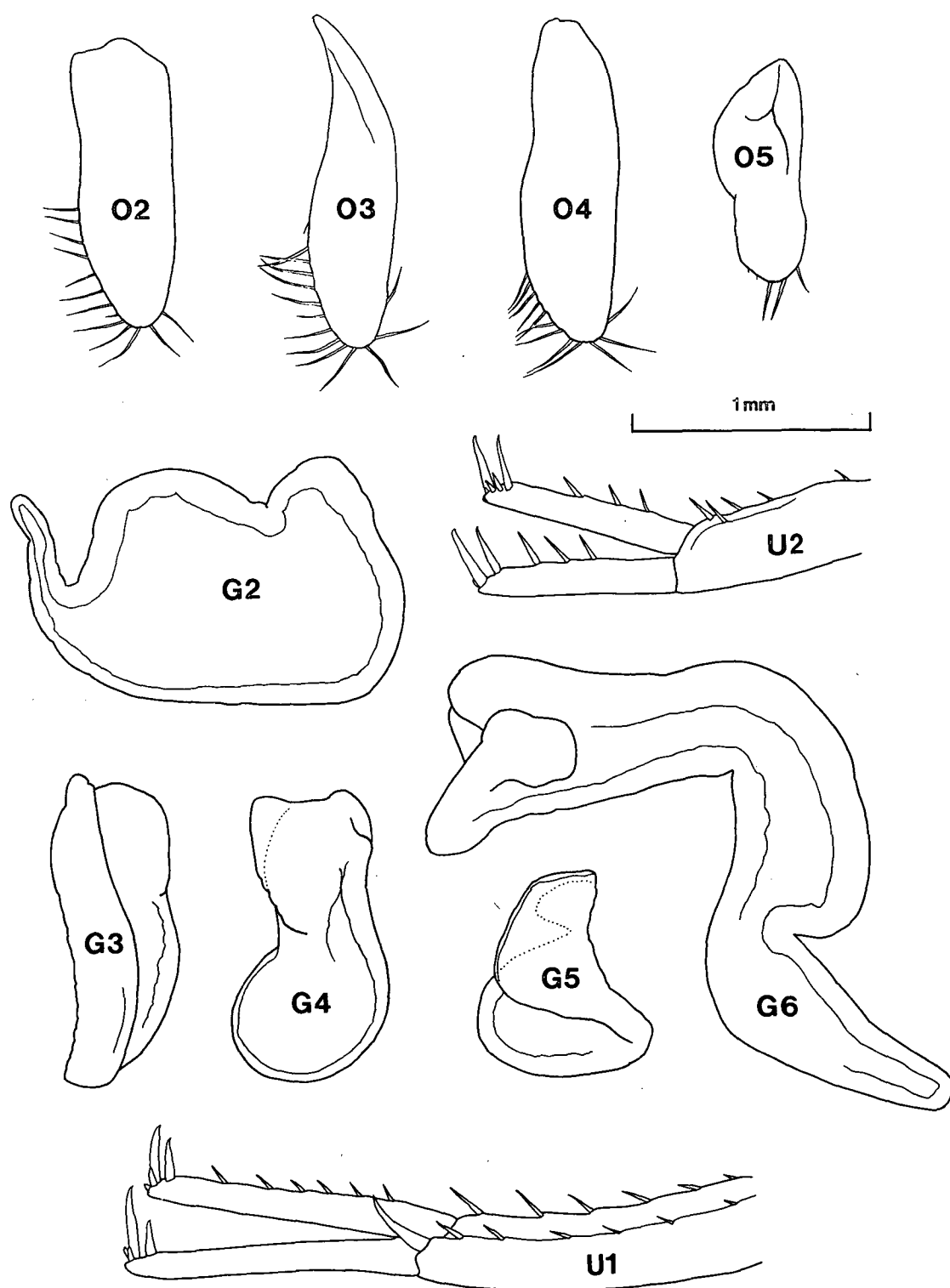


FIGURE 3.24 *Austrotroides longicornis* sp.n., holotype ♀.

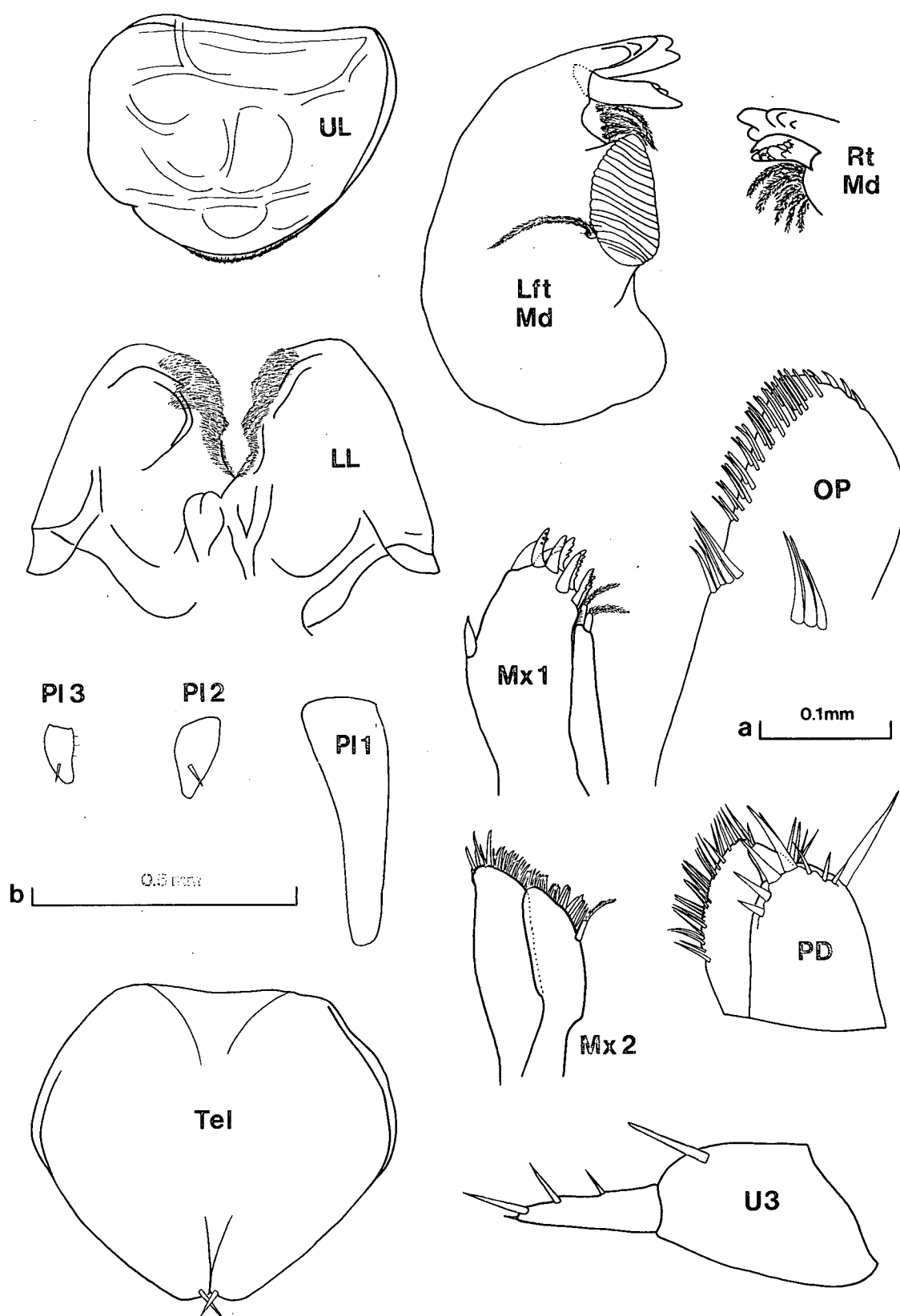


FIGURE 3.25 *Austrotroides longicornis* sp.n., holotype ♀. Scale a; OP, PD. Scale b; Lft Md, Rt Md, Mx1&2, UL, LL, Tel, U3, P11-3.

Male:

Length 10.1 mm. Antenna 1, flagellum 9-segmented [most found; 9], antenna 2 with 29 segments [most found; 29]. Like female, but bearing paired ventral penes and lacking oöstegites.

Remarks

This species, with its distinctive long antennae (to which its name alludes) and uropods (especially uropod 3) is apparently quite rare (see Chapter 4). It bears most similarity in morphology to *A. maritimus* sp.n. (q.v.).

Austrotroides leptomerus, sp.n.

Figures 3.26 - 3.29

Types

Holotype ♀ (ovig., 4 eggs); Top of ridge 2 km W. of Surprise Bay, South Coast Track, S. Tasmania. Beside track in dry woodland. UGR 8210-708757. Coll. JAF 28.xii.1975 (8210-9). Allotype ♂; Beside Old Hartz Track at head of Arve R., W. of Taylor's Ridge. Ex dry *Richea pandanifolia* foliage. UGR 8211-829146 Coll. JLH, AMMR 24.viii.1973 (8211-27). Paratypes 6 ♂♂, 2 ♀♀; same data as allotype.

Other material examined: TASMANIA:

7913-8(1)

8012-23(3), -65(1)

8110-15(1)

8210-8(1)

8211-28(2)

Diagnosis

A large, slender-bodied landhopper, with elongate antennae and peraeopods, large eyes, sexually similar gnathopods and pleopods reduced to vestigial stumps.

Description

Female:

Length 14.5 mm, ovigerous, with 4 eggs. Head just longer than deep; eye large, almost round, width more than one-third head length, anteriorly placed. Antenna 1 very long, reaching four-fifths of the way along last segment of antenna 2; flagellum longer than peduncle, comprising ten segments [most found; 11]. Antenna 2 very long, slender, longer than head and first five peraeon segments, peduncular segment 5 slender, longer than rest of peduncle; flagellum of 27 segments [most

found; 29], bearing 4 groups of 3 short setae.

Upper lip fairly deep, pilose apically, with lateral pilose patches; indentation of right margin not discernible. Lower lip deep, some sparse pilosity on outer margins, inner shoulders and central trough margins thickly pilose; lateral lobes slender. Left mandible 5-cusped, lacinia mobilis 5-dentate, molar with 18 striations. Right mandible with 4 cusps, lacinia with 2 teeth. Maxilla 1, inner plate narrowing distally; outer plate narrow, 2-segmented palp distal of midway along outer margin, apical spine-teeth short, dentition formula 2-2-1-3-4-4-4-4-5. Maxilla 2, outer plate much broader than inner, which is armed distally with numerous short spines, slightly longer at inner end, plumose seta prominent; outer plate bearing several small spines on outer margin, four large sharp spines near the apex.

Maxilliped, inner plate fairly narrow, apical spine-teeth prominent, inner quite small; lateral surface with a group of six small plumose spines, inner margin of medial surface with seven plumes, and two submarginal plumose spines distally. Outer plate narrow, rounded apically, submarginal spines small, mostly blunt-tipped. Palp fairly broad, lobe of segment 2 distally crenulate, spinose; spines of segment 3 mostly distal, some rather stout; segment 4 very small, masked by distal section of lobe of previous segment.

Gnathopod 1, coxal plate shallow, inner shelf weak, lower margin spinose. Segment 2 spinulose anteriorly. Segment 5 long, deeply tumescent posteriorly, medial surface bearing a group of small spines. Segment 6 shorter than 5, gently narrowing distally, lightly spinose behind, anterior margin with three groups of spines, very short palm exceeded by strong dactyl.

Gnathopod 2, coxal plate broad, spinulose below, posterior process elongate, acutely pointed. Gill large, anterior extension long, slender; oöstegite broad, three-quarters as long as segment 2, 12 slender setae set near apex and back along anterior margin to near midpoint. Segment

2 slender, elongate, spinose anteriorly. Segment 4 short, posterodistal tumid lobe small. Segment 5 very long, slender, very weakly spinose, posterior lobe shallow and long. Segment 6 very slender, elongate but shorter than 5, medial spine-row comprising tiny spinules, distal lobe small, dactyl weak, longitudinal.

Peraeopod 3, coxal plate broad, shallow, posterior lobe elongate, acutely pointed. Gill quite broad, sac-like, oöstegite broadening distally, 17 slender setae near apex and along anterior margin. Segment 2 linear, poorly spinose, segments 4-6 elongate, spinose behind, dactyl slender, terminal spine curved.

Peraeopod 4 similar, but coxal plate broader and shallower, oöstegite also bearing 17 setae.

Peraeopod 5, anterior coxal lobe broad, shallow, rounded and spinulose below; posterior lobe just shallower, strongly rounded distally. Gill small, bilobate; oöstegite just over half as long as those of peraeopods 3 and 4, narrowing to the rounded apex which bears three spinules. Segment 2 small, slender-ovate, serrulate and spinose behind. Segments 4-6 long, spinose in front; dactyl long, slender, terminal spine curved.

Peraeopod 6 coxal plate small, posterior lobe shallow, semicircular below. Gill long, anseriform but "neck" strongly curved anteriorly, distally tapering and margins broadly crenate. Segment 2 slender-oblong, distal lobe very shallow and broad, hind margin distally spinose. Segments 4-6 elongate, slender, spinose, dactyl slender, terminal spine almost straight.

Peraeopod 7, coxal plate small, smooth below. Segment 2 small, distal margin meeting trunk of segment subapically, but forming very small subdistal lobe. Segments 4-6 very elongate, slender, with numerous spine-groups; segment 6 with eleven on each margin. Dactyl slender.

First epimeral plate deep, narrow, rounded below, convex behind. Second plate projecting well beyond first and third, broadening distally,

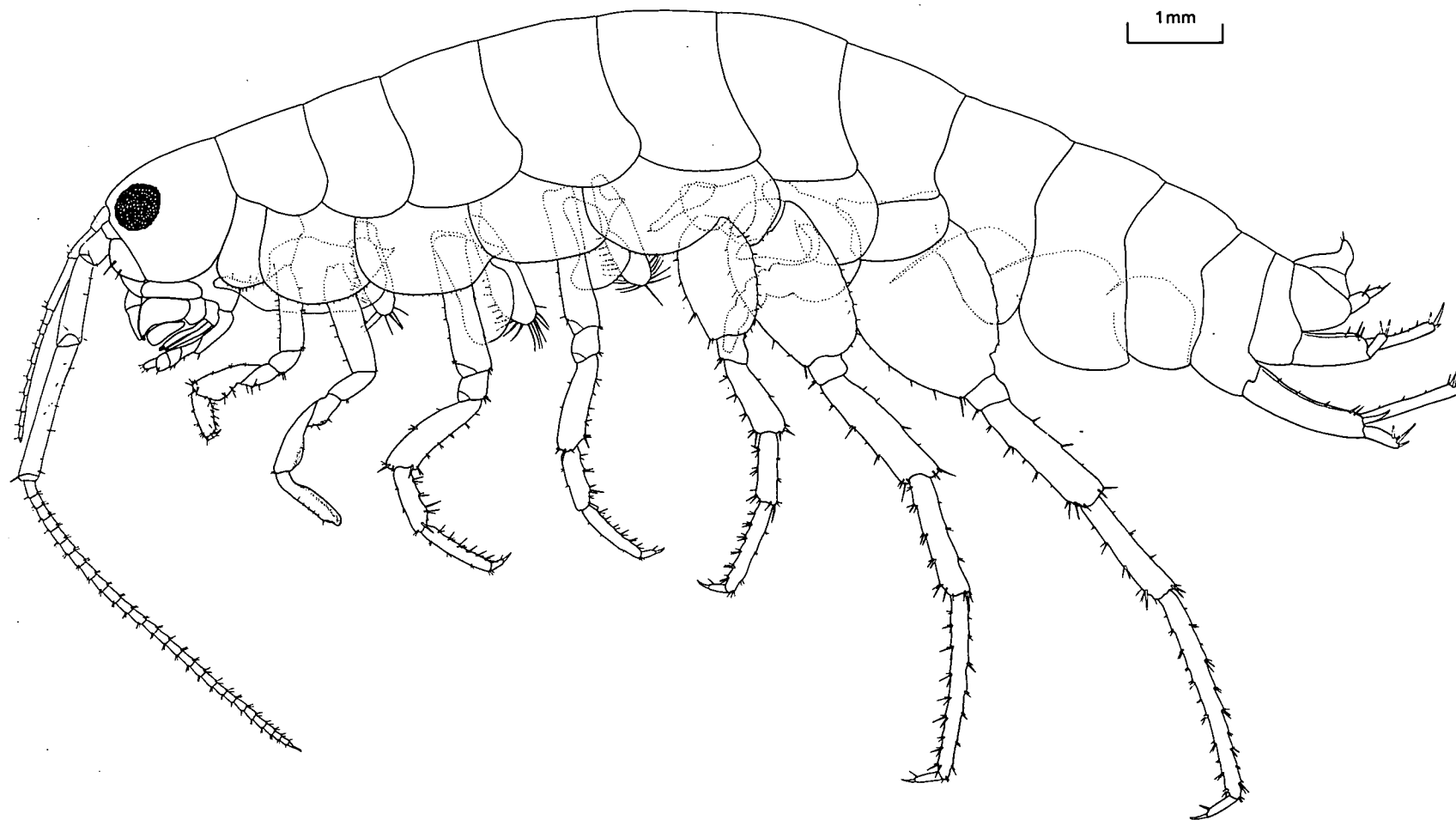


FIGURE 3.26 *Austrotroides leptomerus* sp.n., holotype ♀.

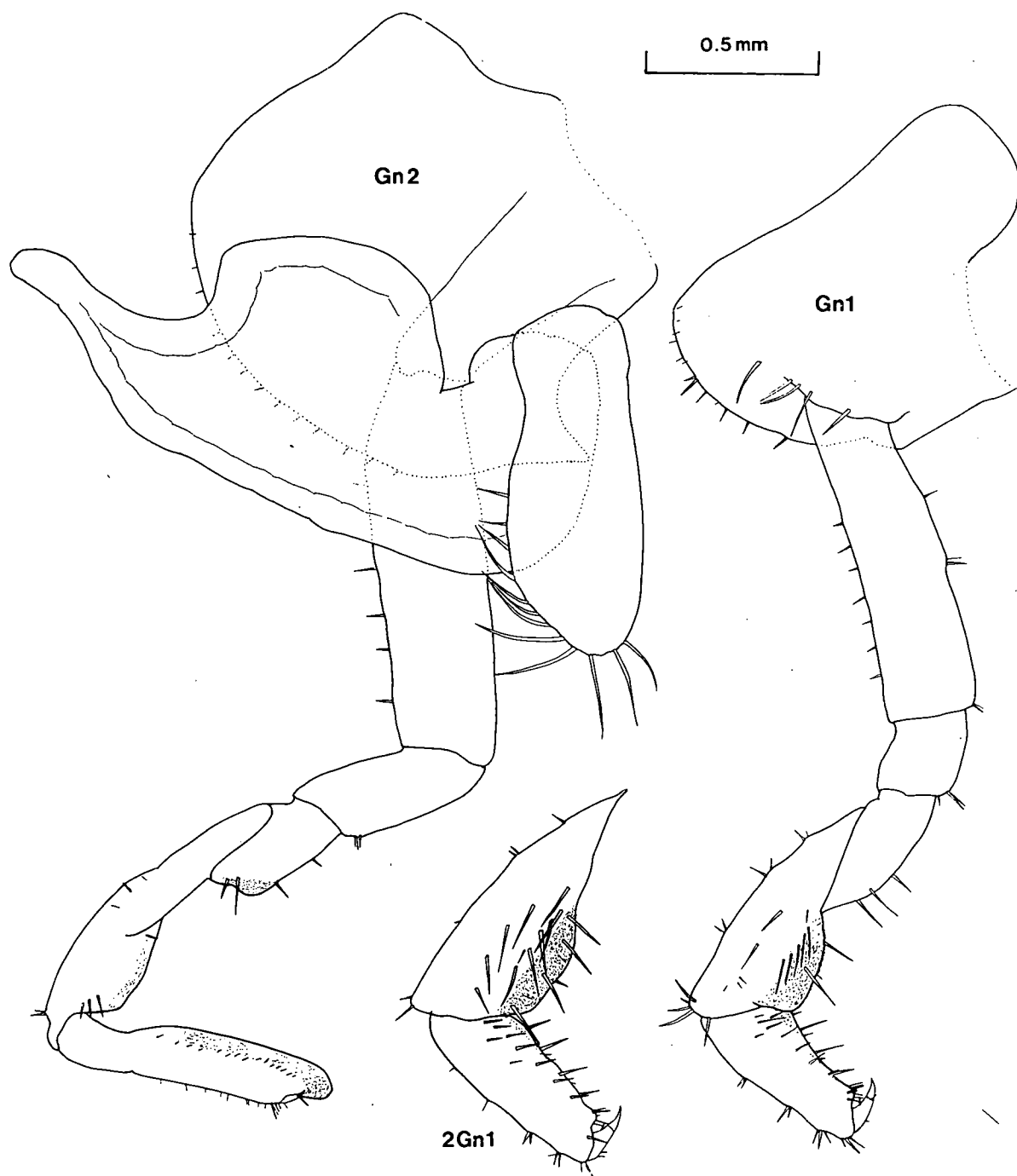


FIGURE 3.27 *Austrotroides leptomerus* sp.n., holotype ♀. 2, allotype o.

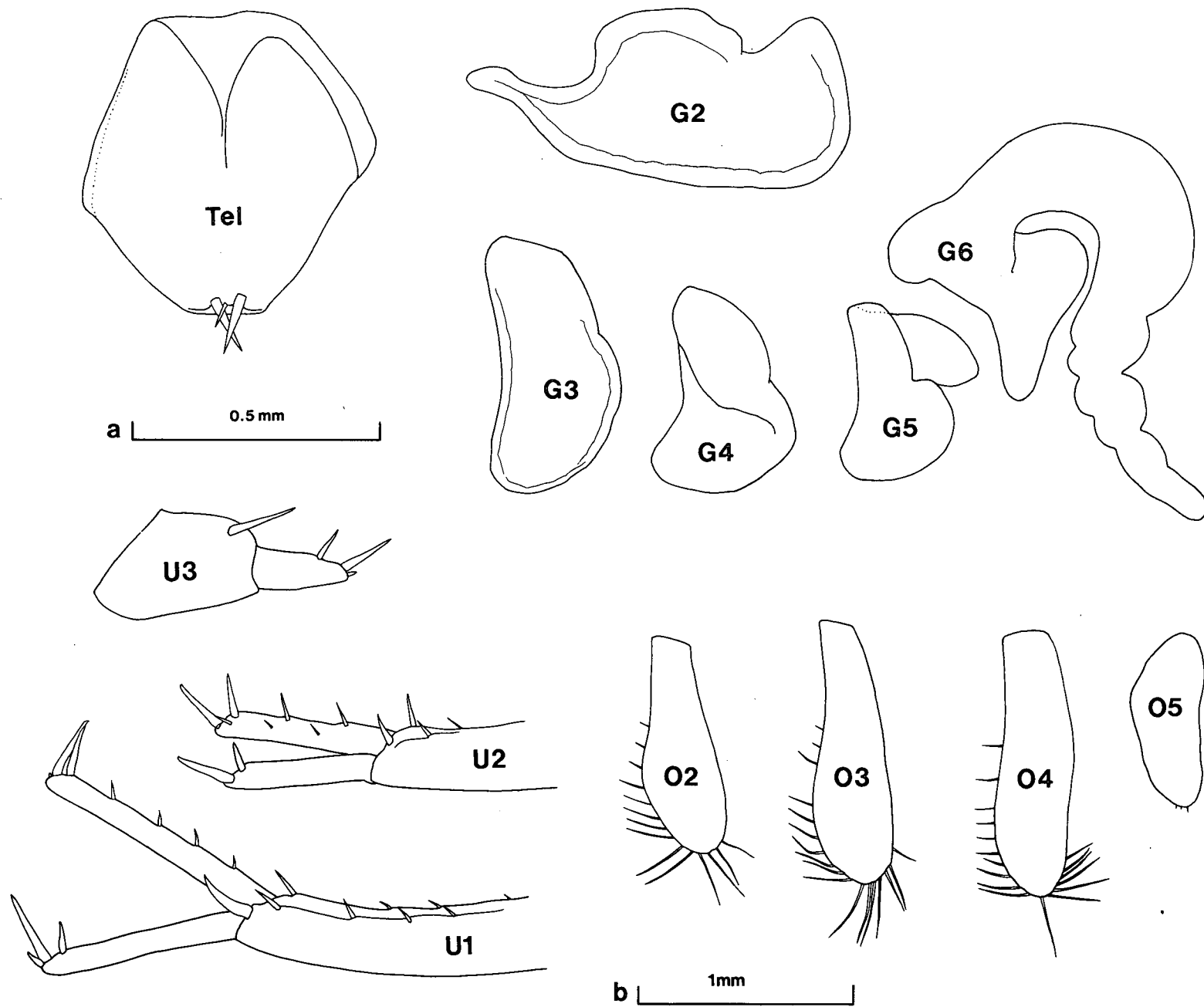


FIGURE 3.28 *Austrotroides leptomerus* sp.n., holotype ♀. Scale a; Tel, U3. Scale b; G2-6, O2-5, U1&2.

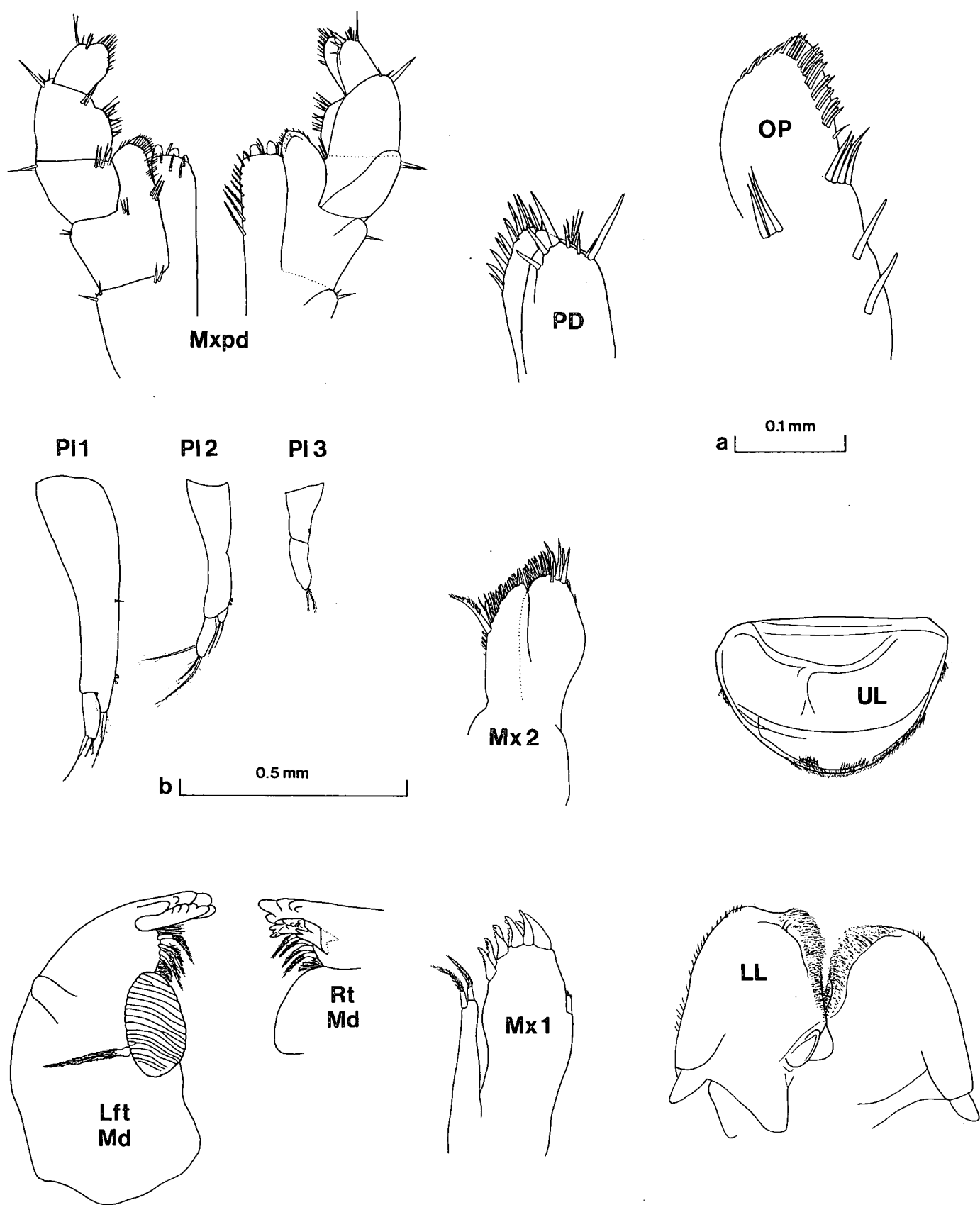


FIGURE 3.29 *Austrotroides leptomerus* sp.n., holotype ♀. Scale a; OP, PD. Scale b; Mxpd, Mx1&2, UL, LL, Lft Md, Rt Md, PI1-3.

round below, produced minutely behind, hind margin straight. Third plate much smaller than second, rounded below, slightly produced posterodistally, hind margin sinuous.

Pleopods all greatly reduced. First pleopod, peduncle narrowing distally, one small spine near midway on inner margin, two coupling spines subapically. Inner ramus the longer, slender, with three small apical plumose setae. Outer ramus fused with peduncle, bearing an apical seta. Second smaller, biramous, with two coupling spines, inner ramus the longer, bearing one subapical and two apical setae, outer with two apical setae. Third even shorter, single ramus as long as peduncle, which bears two coupling spines; ramus with two short apical setae.

Uropod 1 elongate, peduncle longer than rami, slender, with three spines on each margin, apical spine strong, short. Outer ramus with naked margins, one of the distal spines slender and longer than peduncular apical spine. Inner ramus subequal to outer, with four marginal spines, two of the distal spines long and slender. Uropod 2 peduncle slender, bearing two spines on each margin. Rami subequal to each other and peduncle, outer ramus with naked margins, inner bearing two sets of two marginal spines, both rami bearing long apical spines. Uropod 3, ramus long, subcylindrical, ramus slender, bearing one subapical and two unequal apical spines.

Telson fairly broad, apically hardly cleft, with a strong spine on each side and a small spine on one side of the apex.

Male:

Length 13.1 mm. Antenna 1 flagellum 12-segmented [most found: 12], antenna 2 flagellum with 34 segments [most found: 34]. Like female but lacking oöstegites and bearing paired ventral penes.

Remarks

The long, slender, distally crenate gills of *Austrotroides*

leptomerus sp.n. are characteristic and easily recognized, as are the large eyes, slender body and long appendages. *A. crenatus* Friend (in MS), a South Australian species, also has crenate gills and bears a number of other similarities to this species, although it is superficially different in terms of the slenderness of the body and relative length of limbs. *A. leptomerus* sp.n. can also be distinguished from *A. crenatus* by features listed above as common to the Tasmanian *Austrotroides* species.

A. leptomerus sp.n. appears to be a rare species, being found in low numbers in litter, at only a few southwest Tasmanian sites. The largest collection, however, was taken from litter caught in the dry head of a dead Giant Grass Tree (*Richea pandanifolia* Hook.f.), so it may be that *A. leptomerus* sp.n. occupies a specialised micro-habitat which has usually been missed in collection. Males and females of this species are of similar size. The specific epithet refers to the slender body which is a very distinctive feature.

Austrotroides maritimus, sp.n.

Figures 3.30 - 3.33

Types

Holotype ♀ (brooding 9 young); Maatsuyker I., off S. coast of Tasmania. Near top of haulage, under teatree. UGR 8110-419669. Coll. JAF 16.i.1979 (8110-4). Allotype ♂; 3 km N. of Cockle Ck., in seaweed, eucalypt and bush litter at high water mark. UGR 8210-912787. Coll. AMMR, BK, DC. 19.v.1976 (8210-14). Paratypes 4 ♂♂, 6 ♀♀ (2 ovig.) 4 imm.; same data as allotype.

Other material examined: TASMANIA:

7913-6(1), -7(68), -8(10)

8011-3(3)

8110-1(63), -2(40), -3(10), -5(2), -7(7), -8(8), -9(14), -10(21),
-11(1), -16(19), -21(11), -22(31)

8210-20(1), -21(2), -22(1)

8411-8(14)

Diagnosis

A large landhopper with deep coxal plates, mitten-shaped second gnathopods in both sexes, hands of first gnathopods secondarily enlarged, especially in males; antenna elongate, and pleopods reduced to vestigial stumps.

Description

Female:

Length 13.8 mm, bearing 9 young [4-9]. Head as deep as long, eye almost round, width one-third head length. Antenna 1 long, slender, reaching two-thirds of the way along last peduncular segment of antenna 2; peduncle longer than flagellum, segment 3 longer than 1 and 2 together;

flagellum of ten segments [3-10]. Antenna 2 as long as head and first four pereopod segments, segment 5 of peduncle over half the peduncular length, slender; flagellum of 27 segments [8-27], each with groups of short bristles.

Upper lip fairly deep, with a small patch of apical pilosity, indentation of right margin prominent. Lower lip narrow, lateral lobes small, inner shoulders moderately pilose, margins of central trough only faintly pilose. Left mandible 4-cusped, lacinia mobilis 4-toothed, molar process 17-striate. Right mandible with 5 cusps, lacinia 2-cusped, with a distal field of minute rounded projections, toothed ridges running towards proximal end. Maxilla 1, inner plate short, narrowing distally, apical plumes strong; outer plate slender, narrowing distally from position of 2-segmented palp, beyond mid-point of convex outer margin; apex narrow, spine-teeth strong, dentate, clustered; dentition formula 0-0-3-2-4-4-4-4-5. Maxilla 2 inner plate narrower than outer, plume near inner margin quite strong, distal spines densely clustered, short at outer end, long at inner end. Outer plate apex armed with 5-6 large sharp spines, several shorter ones outside these and submarginally; other spines of medium length.

Maxilliped inner plate slender, broadening distally to rounded apex, which bears three unequal bluntly rounded spine-teeth, five plumose spines set on the outer distal margin; inner margin with a row of ten plumose spines, four submarginally near inner distal corner. Outer plate apically rounded, submarginally profusely spined, proximal groups of long spines strong. Palp fairly strong, lobe of second segment narrow but bearing four groups of spines near inner margin; third segment with a broad lateral and distal lobe which masks the slender, conical fourth segment; mediobasal spines of third segment strong.

Gnathopod 1, coxal plate distally spinulose, inner shelf bearing a row of slender spines. Segment 2 elongate, broadening distally,

spinose in front. Segment 3 with negligible posterior blister. Segment 4 quite broad, spinose on posterior margin, medial surface bearing many slender spines; tumid lobe fairly deep. Segment 6 sub-equal to 5, swollen and very spinose behind; palm very oblique, defined by two strong spines between which the powerful dactyl closes.

Gnathopod 2, coxal plate large, deeper than broad, distally smoothly convex and spinulose, posterior process prominent, acute. Gill large, proximally broad, anterior extension short, slender; oöstegite broad, just shorter than segment 2, with 12 small slender setae near the apex. Segment 2 slender, broadening distally, anterior margin spinose. Segment 3 longer than 4, which has a large posterodistal tumescence. Segment 5 slender, elongate, with a shallow, broad posterior blister and a row of slender spines distal of this, on the medial surface. Segment 6 long and slender, medial spine-row double, composed of many small spines, distal lobe long.

Peraeopods 3 and 4, coxal plates large, deeper than broad, distally spinulose, posterior process prominent, sharp. Gills quite large, sac-like; oöstegites broad, longer than that of gnathopod 2, with 10-12 small setae near the apex. Second segments almost linear, segments 4-6 spinose behind, dactyls slender.

Peraeopod 5, coxal plate very large, anterior lobe broad and deep, distally rounded, spinulose; posterior lobe much smaller, shallower, almost straight behind. Gill small, bilobed, oöstegite over half as long as those of peraeopods 3 and 4, half as broad as long, distally bearing four small and two tiny setae. Segment 2 slender, oblong, posterior margin serrate, spinose. Segments 4-6 slender, spinose in front; dactyl slender, terminal spine curved.

Peraeopod 6, anterior coxal lobe small, distal margin straight, posterior lobe deep, broad. Gill long, anseriform, lobate proximally, distal section broad, then narrowing to the blunt apex. Segment 2 narrow, oblong, posterior margin serrulate, spinose, just convex, distal

lobe broad but shallow. Segments 4-6 slender, spinose anteriorly, dactyl small and slender.

Peraeopod 7, coxal plate deep, anterior margin concave, spinulose, forming a blunt anterior projection, lower margin rounded, serrulate posteriorly. Segment 2 fairly slender, hind margin serrulate, curving round to meet trunk of segment subapically, forming a shallow subdistal lobe. Segments 4-6 slender and rather spinose, dactyl small, slender.

First epimeral plate deep, convex and serrulate behind. Second plate markedly longer than third, both rounded in front and below, hind corner sharp, obtuse, hind margin straight and serrulate.

Pleopods all reduced to vestigial stumps, representing peduncle only. First pleopod narrowing distally bearing four spinules arrayed longitudinally and submarginally. Second pleopod, about half the length of first, with four spinules, third still smaller, a small slender stump, bearing two submarginal spinules.

Uropod 1 slender, peduncle longer than rami, with three inner and four outer marginal spines, apical spine slender, curved; rami very slender, subequal, apical spines long, outer ramal margins naked, inner bearing three spines and a spinule. Uropod 2, peduncle slender, as long as subequal rami, bearing three inner, three outer and an apical spine; outer ramal margin with three spines, inner bearing two. Uropod 3 peduncle subcylindrical, armed with a large and a small slender spine; ramus slender, with two marginal spines and a large and two small spines on the apex.

Telson just longer than broad, apex slightly cleft and provided with two unequal spines on each side.

Male:

Length 12.2 mm. Antenna 1 flagellum of 9 segments [3-9], that of antenna 2, 28-segmented [8-28]. Gnathopod 1, coxal plate broad, inner shelf bearing long slender spines. Segment 2 strong, broadening distally,

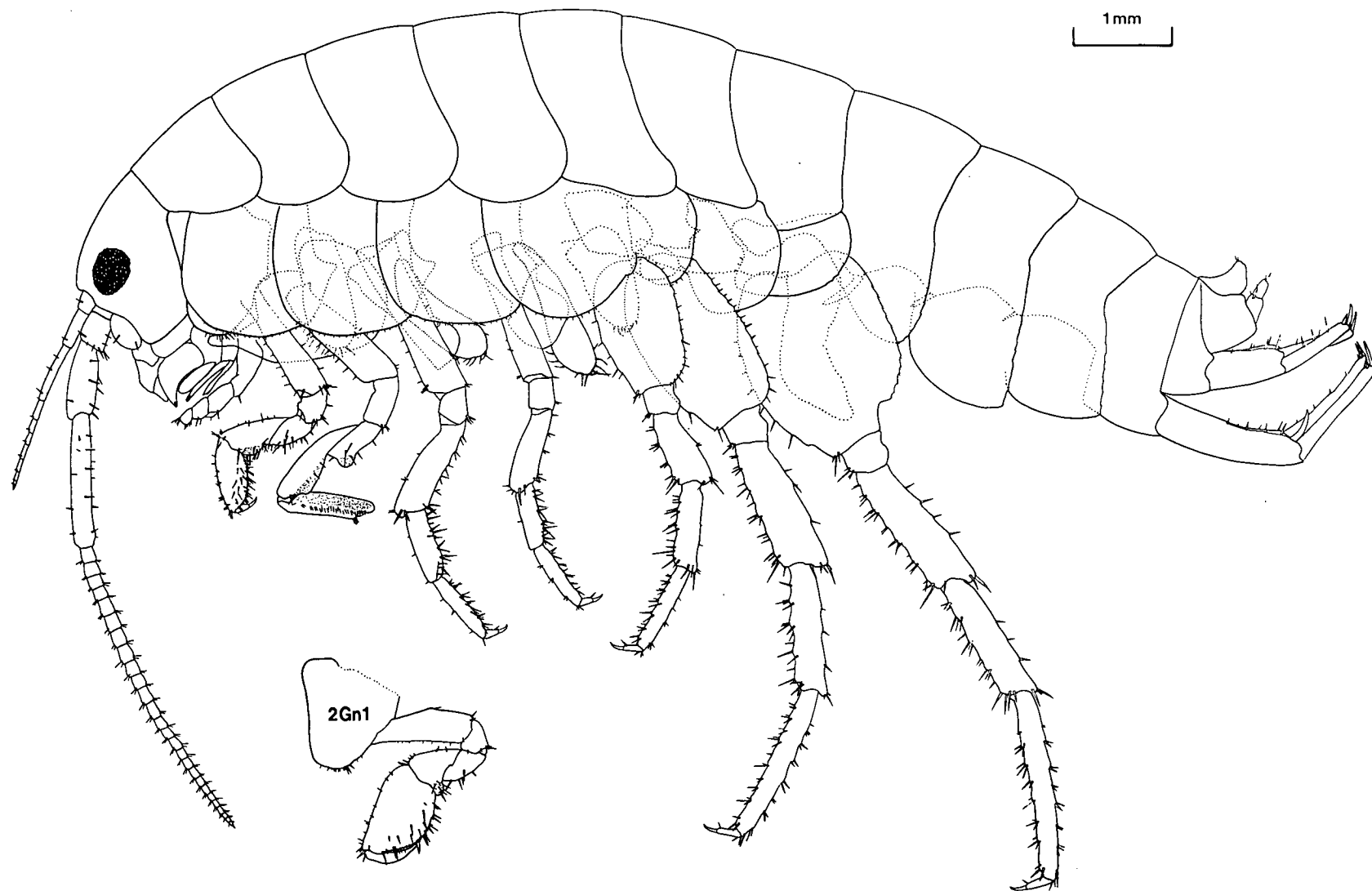


FIGURE 3.30 *Austrotroides maritimus* sp.n., holotype ♀. 2, allotype ♂.

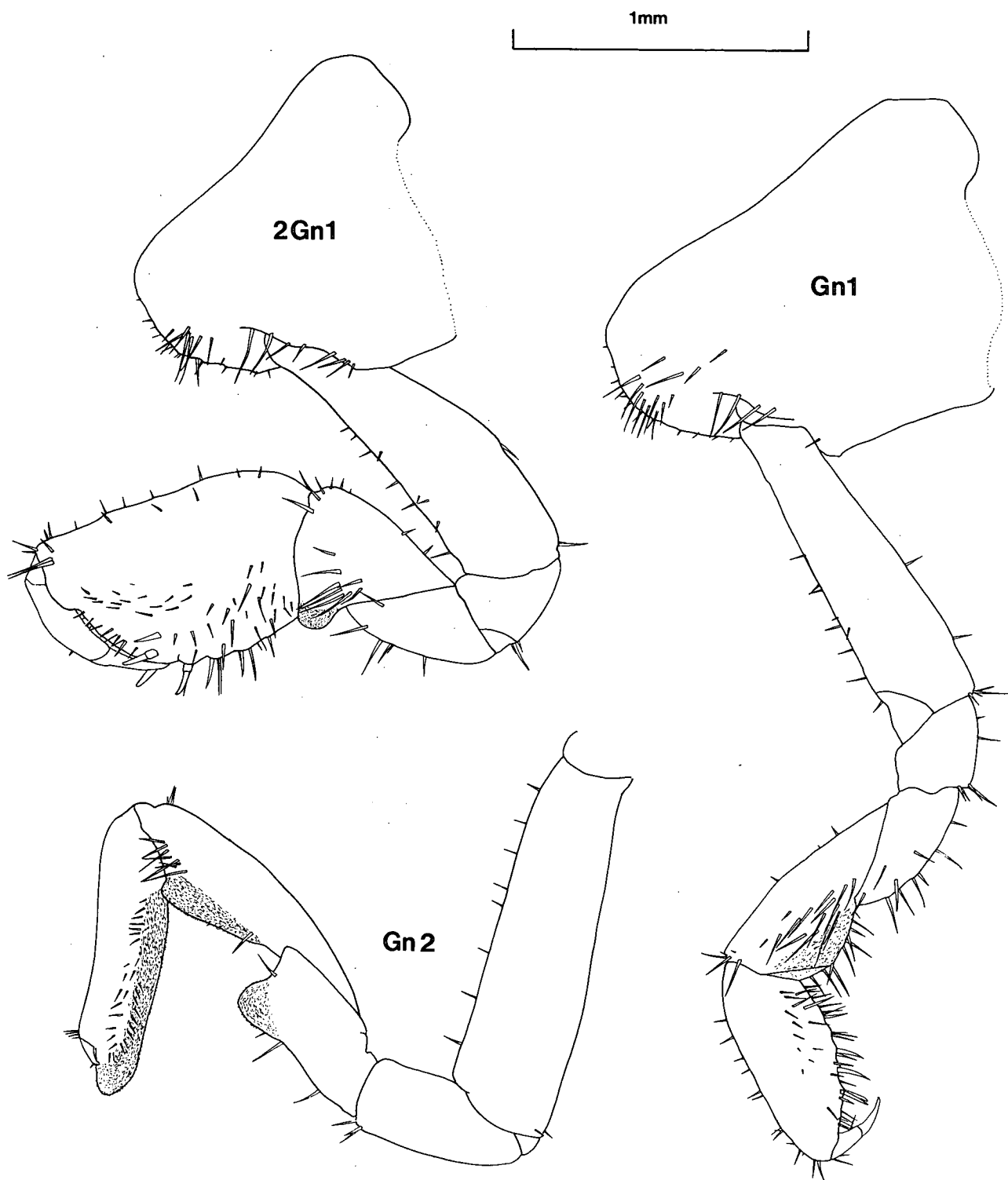


FIGURE 3.31 *Austrotroides maritimus* sp.n., holotype ♀. 2, allotype ♂.

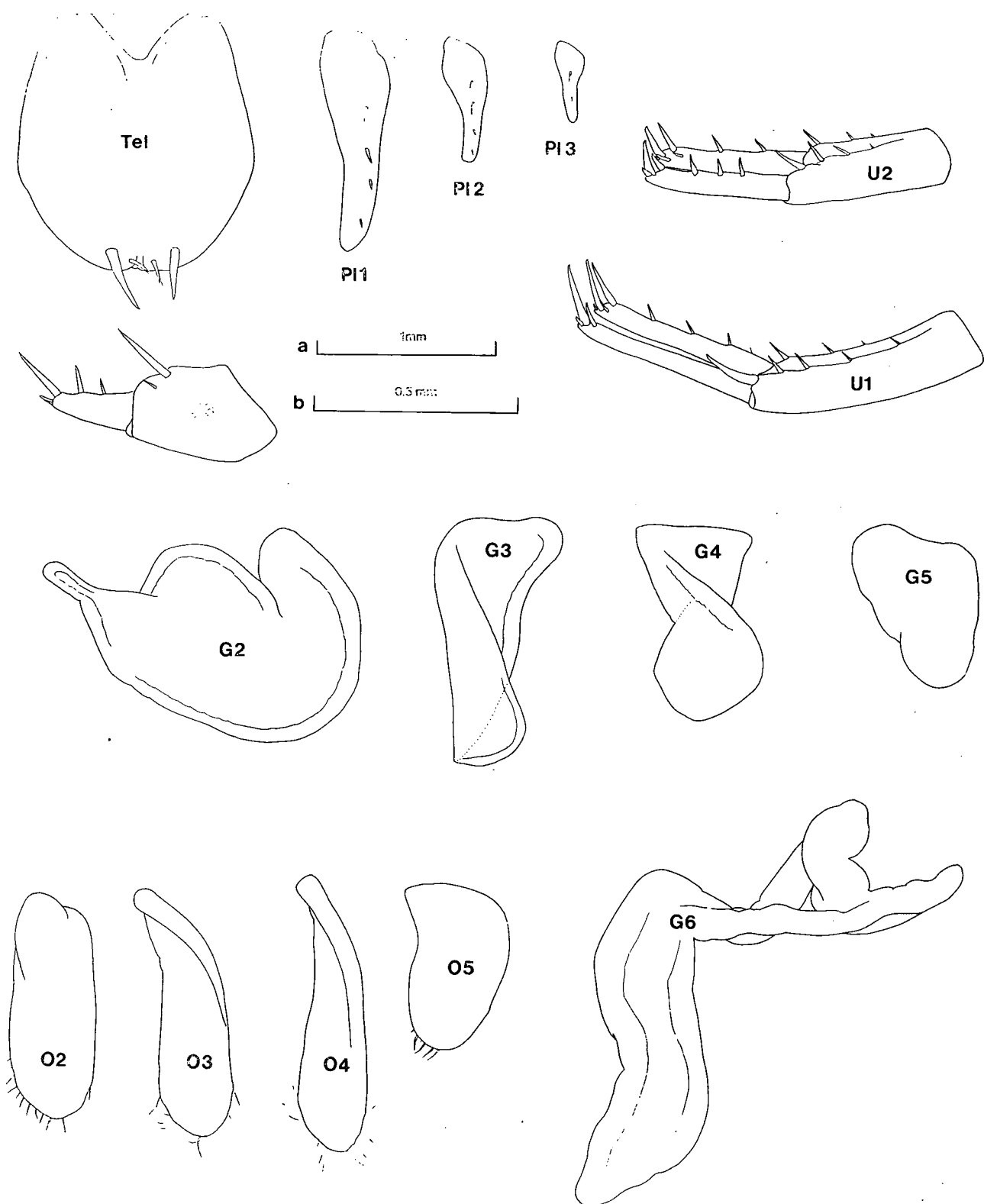


FIGURE 3.32 *Austrotroides maritimus* sp.n., holotype ♀. Scale a; U1&2, G2-6, O2-5. Scale b; Tel, U3, P11-3.

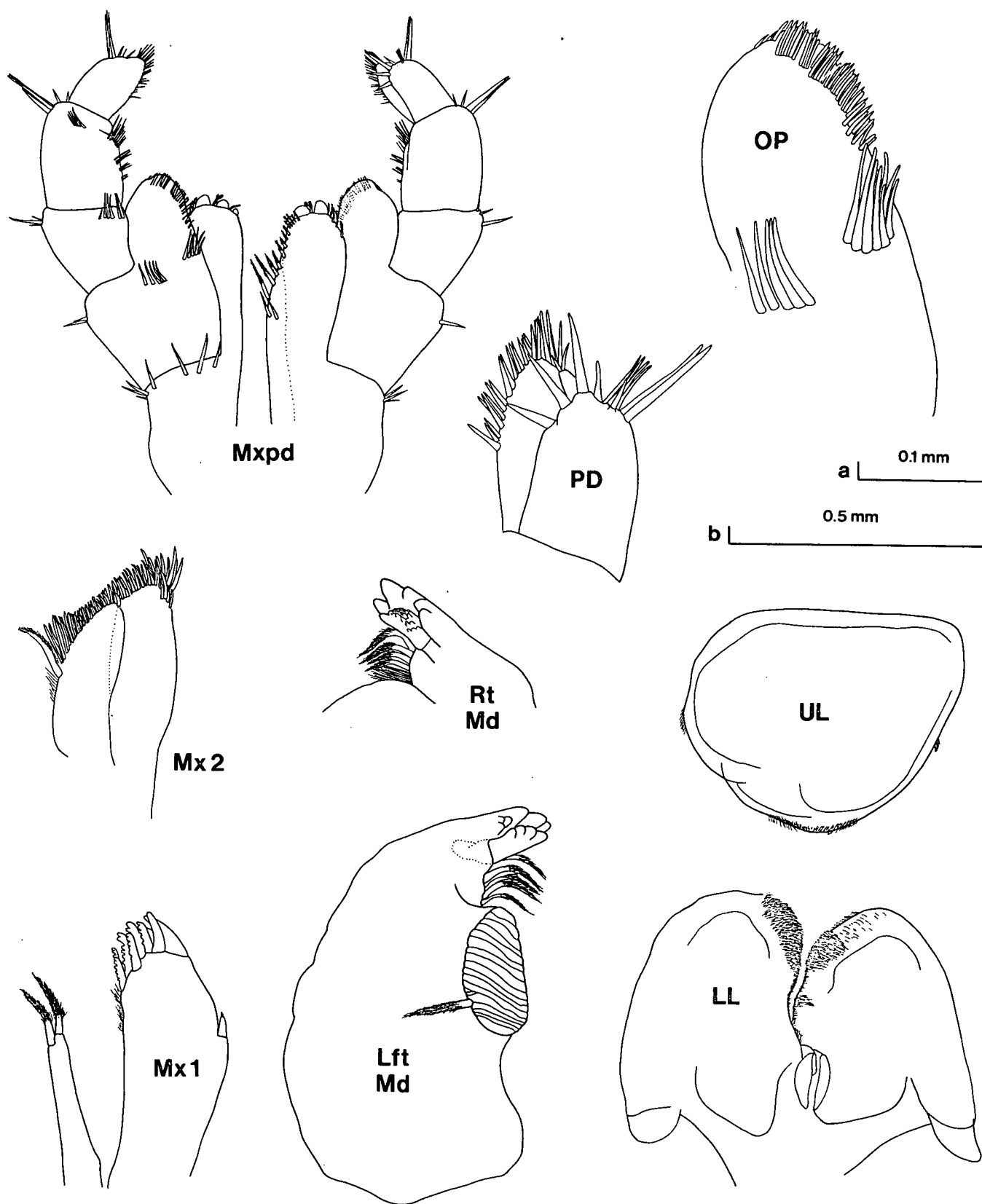


FIGURE 3.33 *Austrotroides maritimus* sp.n., holotype ♀. Scale a; OP, PD. Scale b; Mxpd, Mx1&2, UL, LL, Lft Md, Rt Md.

convex behind. Segments 3 and 4 short and broad, 4 with a small posterior tumid lobe, spinose. Segments 6 and 7 forming a powerful subchelate hand; segment 6 greatly swollen, two-thirds as broad as long, spinose behind; distally forming a convex, lightly spinose palm, defined by two stout spines, between which the very powerful dactyl closes, exceeding the palm.

Otherwise like female, but lacking oöstegites and bearing ventral penes.

Remarks

Segment 6 of the first gnathopod of *A. maritimus* sp.n. is unusually large in males and swollen in females, and this is immediately obvious in adult specimens. Similar features have developed in several other landhopper species (see *Mysticotalitrus tasmaniae*, (Ruffo), Remarks, below) and appears to be important in systematics only at the species level. In other characters, *A. maritimus* sp.n. is very similar to *A. longicornis* sp.n.; however, it lacks the long appendages of the latter species, its peraeopod 6 gill is not as strongly incised posteriorly, and the telson bears only small apical spines, unlike the large prominent pair of *A. longicornis* sp.n.

On the mainland of Tasmania, *A. maritimus* sp.n. is only found within a few metres of the supralittoral zone, and it is to this restricted occurrence that the specific epithet refers. The species is apparently limited to areas of high ionic concentration, as it is only found any distance from the sea on small exposed islands, such as Maatsuyker I., where sea-spray is blown a long way inland.

Genus *Mysticotalitrus* Hurley 1975 (stat. nov.)

Talitrus (*Mysticotalitrus*) Hurley 1975a p.162.

Diagnosis

Large landhoppers, primarily showing no sexual dimorphism, with distinctive maxillipeds, gills, pleopods and epimeral plates. Antennae fairly long, eyes large; upper and lower lips broad, shallow, sparingly pilose; maxilla 1 broad, inner plate short, outer plate with tiny palp, apical spine-teeth well separated, innermost leaning inwards; maxilla 2 broad, plumose seta long, apical spines short, separated. Maxilliped inner plate with large outer spine-teeth, few plumose setae; outer plate outer margin arcuate, sharp apex bearing a group of spines, inner margin with spine groups; palp segments 2 and 3 bearing narrow lateral lobes with groups of inner marginal spines, segment 4 not masked, broad. Gnathopod 1, hand basically simple, segment 6 almost linear; secondarily swollen in *M. tasmaniae*, more so in ♂. Gnathopod 2 minutely chelate in both sexes, hand slender, linear, terminal lobe subacute, dactyl small. Peraeopods 6 and 7 long, dactyls elongate. Anterior and posterior gills large, gnathopod 2 gill with slender distal extension, peraeopod 6 gill complex, folded, lobate. Oostegites mostly slender, posterior pair short, thick and fleshy. Epimeral plate 2 much the longest, of distinctive shape; pleopods biramous, reduced, of similar size. Uropods 1 and 2, outer ramal margins naked, uropod 3 small.

Type species: *Mysticotalitrus tasmaniae* (Ruffo)

Distribution: Tasmania

Other species: *M. crypticus* sp.n.

Remarks

The taxon *Mysticotalitrus* was set up as a subgenus by Hurley (1975a) in his subdivision of the genus *Talitrus*. He chose *T. tasmaniae* Ruffo

as the type species and included also the species *T. fernandoi* De Sylva 1959 and *T. trukana* Barnard 1960. All these species were described on the basis of females only; also Ruffo's specimens were damaged, and De Sylva's drawings are of little help in determining the morphology of his species. Hurley selected nine distinctive characters to delimit the subgenus. Three of these, "pleopods 1 and 2 biramous or reduced", "pleopod 3 biramous or vestigial", and "uropod 2 rami equal or unequal" do little to help define the group. Three of the characters do not apply to the type species, *T. tasmaniae* (redescribed below): these are "uropod 1 interramal spine absent", "telson sparsely spined, spines marginal" and "peraeopod 4 [=Pr6] gill small". The three remaining features are "maxilliped...outer plate distally convex", "epimeral plate 3 normal" and "uropod 3 ramus a small conical segment, large spine on peduncle, 2 terminally on ramus". The name *Mysticotalitrus* stays with *T. tasmaniae*, but several differences more significant than the three similarities above can be found between this species and the two others in Hurley's subgenus. Hurley (1975a) admits that the *Mysticotalitrus* grouping is his least convincing, and the highly disjunct nature of its distribution (Tasmania, Sri Lanka and Micronesia) makes its reality more dubious.

The morphology of *T. fernandoi* is poorly known due to the low quality of the original drawings and description, but it is possible to distinguish several characters which separate it generically from *T. tasmaniae*. These are the possession of vestigial pleopods, the distally truncate maxilliped outer plate bearing a row of spines, and the extremely small size of the adult female (length 2.3 mm).

It has been suggested (Barnard, 1960; Bousfield, 1971) that *T. trukana* is really a member of the sexually dimorphic group of land-hoppers. The broad maxilliped palp, submarginal spine-row on the outer plate, deep, narrow upper and lower lips and maxillae, short, deep distal segments of ♀ gnathopod 2 and sac-like gills support this

view. Other major differences which require the generic separation of this species from *T. tasmaniae* include:

- antenna 1 very short, geniculate;
- maxilla 2 spines long;
- maxilliped palp, fourth segment masked;
- gnathopod 1, segment 6 slender, almost linear, with a small oblique palm exceeded by dactyl;
- slender pleopods;
- uropod 1 lacking an interramal spine;
- uropod 2 outer ramus with a spine.

The existence in Tasmania of a species closely related to *T. tasmaniae* further indicates that *Mysticotalitrus*, excluding *T. fernandoi* and *T. trukana*, is a discrete endemic entity, recognized here at the generic level.

Mysticotalitrus tasmaniae (Ruffo)

Figures 3.34 - 3.37

Parorchestia ? sp. Hunt 1925 p.859, figure 5.*Talitrus* (subg. ?) *tasmaniae* Ruffo 1949a, p.207,
figures I(1-9), II(1-3)*Talitrus tasmaniae* Hurley 1955 p.147*Talitrus (Mysticotalitrus) tasmaniae* Hurley 1975a pp.160, 162.

Types

Syntypes 2 ♀♀ (ovig.), Museo Civico di Storia Naturale, Genova, Italy; Mt. Wellington, Hobart Town (Tasmania). Coll. O. Beccari and E. D'Albertis, 12.ii.1878 (Not examined).

Other material examined: TASMANIA:

♂ described; ♀ described; 29 ♂♂, 32 ♀♀ (14 ovig.), 5 imm.;

Near Brown's Road, Fern Tree, Mt. Wellington. In litter in area of eucalypt forest unburnt in 1967 fires, above Pipe Track. UGR 8312-197470. Coll. JAF, 2.ii.1979 (8312-12).

♀ (ovig.), National Museum of Victoria, Melbourne; Kingston, leaf mould. Coll. C.Oke, 14. v.1948.

8112-15(1)

8113-2(57)

8210-6(11), -24(2)

8211-5(2), -6(1), -8(2)

8212-10(1)

8213-1(3)

8311-6(6), -7(2)

8312-2(8), -7(107), -10(9), -13(2), -15(11), -16(21), -17(4), -19(36)

8411-1(42), -2(14), -3(3), -5(1), -6(10), -7(9), -9(43)

8412-5(5), -10(7), -16(1)

8413-1(1), -2(2), -5(1), -6(2), -14(1), -21(1)

8512-6(12)

8513-1(12), -3(2), -5(1)

Diagnosis

A large landhopper of the genus *Mysticotalitrus* with swollen first gnathopods, especially in the ♂; second and third epimeral plates posterodistally rounded, telson bearing apical spines only.

Description

Female:

Length 13.0 mm, ovigerous, with 6 eggs [2-8]. Head longer than deep, eye large, width over one-third head length. Antenna 1 reaching over one-third of the way along last peduncular segment of antenna 2; flagellum shorter than peduncle, consisting of six segments [3-6]. Antenna 2 long, almost as long as head and first five pereon segments, last peduncular segment very long, far exceeding rest of peduncle; flagellum longer than peduncle, 22-segmented [8-25], narrow segments with 4 groups of 3 slender setae.

Upper lip broad, lightly pilose apically, indentation of right margin prominent. Lower lip also broad, lateral lobes short, pilosity, confined to inner shoulders. Left mandible 5-cusate, lacinia mobilis bearing 4 teeth, molar with 16 striations; right mandible 5-cusate, lacinia 3-dentate. Maxilla 1, inner plate fairly stout, short, terminal setae short; outer plate broad, palp minute, two-segmented, near midpoint of outer margin, spine-teeth strong, curved, mostly dentate, innermost spine-tooth leaning inwards; dentition formula 0-0-3-3-3-3-4-3-3. Maxilla 2, broad, outer plate broader than inner; inner plate terminal spines short, strong, slightly longer at each end of row, plumose seta large; outer plate a little longer than inner, bearing a row of seven short spinules on the distal outer margin, two large and three smaller spines near the apex, the other spines in the row being sharp and longer than inner plate spines.

Maxilliped, inner plate slender, apex truncate, bearing three fairly large unequal spine-teeth and a blunt spine, medial surface with a row of four short plumose setae near the inner margin, lateral surface bearing two large plumose setae subapically. Outer plate just exceeding spine-teeth of inner plate, outer margin arcuate, apex acute, bearing a group of sharp spines; inner margin armed with ten spines in five evenly-spaced pairs. Palp segments 2 and 3 fairly broad, with narrow lateral lobes, both bearing several small groups of spines; segment 4 projecting well beyond lobe of segment 3, strong, bearing two apical spines; medial spines of segment 3 large.

Gnathopod 1 coxal plate deep, distally rounded and spinose. Segment 2 sublinear, slightly broadening distally, both margins spinulose. Segment 5 as long as 6, medial surface bearing a group of long spines, posterior tumid lobe shallow and broad. Segment 6 swollen, forming a strong sub-chelate hand, spinose on and near undulating hind margin; dactyl strong, terminal spine long and curved, exceeding poorly defined oblique palm; dactyl closes between two strong spines at the posterior end of this palm.

Gnathopod 2, coxal plate deep, rounded and spinulose below, posterior process large, acute. Gill large, broad proximally, anterior extension long, slender; oöstegite broad, long, narrowing distally, bearing ten short marginal setae near apex and along anterior margin. Segment 2 linear, spinulose in front, slightly broader distally; segment 4 with a very small posterior lobe, spinose behind. Segments 5 and 6 subequal, segment 5 slender, hind lobe broad and shallow. Segment 6 long and slender, medial spine-row composed of small spines, dactyl small, distal lobe narrow, subacute.

Peraeopod 3 quite long, coxal plate fairly broad, spinulose below, posterior process small, rounded. Gill elongate, sac-like, oöstegite long, slender, eight setae near the apex. Segment 2 long, segments 4-6 quite long and slender, dactyl small, terminal spine long, distally curved.

Peraeopod 4 similar to 3 but coxal plate straighter below, posterior

process larger, with blunt apex, gill smaller. Segments 2, 4 and 6 shorter.

Peraeopod 5, relatively long, reaching halfway down segment 5 of peraeopod 6, anterior coxal lobe large, anterodistally oblique, straight and spinulose, posterior lobe just shallower but much smaller, concave behind. Gill bilobate, oöstegite half as long as others but much broader, with two spinules on the rounded apex. Segment 2 narrowing distally, hind margin straight, spinulose. Segments 4-6 slender, 6 quite long, dactyl small but terminal spine rather long, curved.

Peraeopod 6, anterior coxal lobe shallow, posterior lobe also shallow, small, rounded below. Gill large, complex, folded and lobate. Segment 2, large, long-ovate, spinulose behind. Segments 4-6 long, fairly spinose, dactyl long, terminal spine long, distally curved.

Peraeopod 7 the longest, coxal plate broad, shallow, smoothly rounded below. Segment 2 large, expanded behind, serrulate hind margin with a distinct, small distal lobe. Segments 4-6 long, dactyl long, about one-third the length of segment 6, terminal spine long, curved.

First epimeral plate shallow, gently rounded below and behind, where margin is weakly serrulate. Second plate distinctly longer than third, gently rounded anterodistally, posterodistally cut away, serrulate convex hind margin curving forward to meet distal margin near middle of plate. Third epimeral plate with strongly rounded front corner, gently convex below, hind corner rounded, serrulate, merging into convex hind margin.

Pleopods all biramous and setose but reduced, decreasing slightly in size posteriorly; each bearing two coupling spines, rami shorter than peduncles, outer ramus longer than inner, segmentation indistinct and fringing plumose setae short. First two peduncles subequal, third shorter, broader, outer margin bearing many very short plumose setae.

Uropod 1 peduncle slender, with two inner and four outer marginal spines, apical spine strong, curved, simple; rami shorter than peduncle, subequal outer lacking marginal spines, inner bearing three; one or two

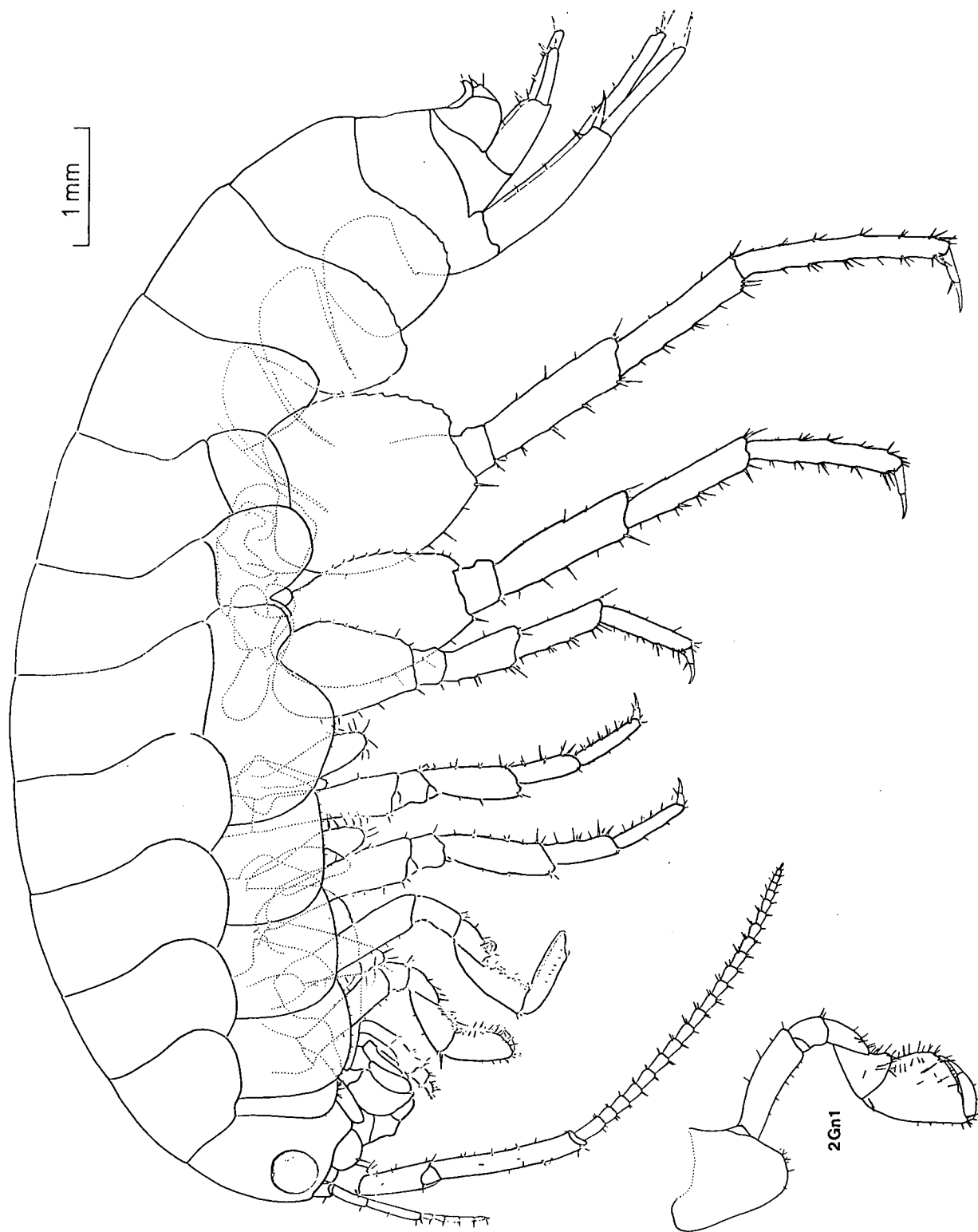


FIGURE 3.34 *Mysticotallitrus tasmaniae* (Ruffo) gen.n., ♀. 2, ♂.

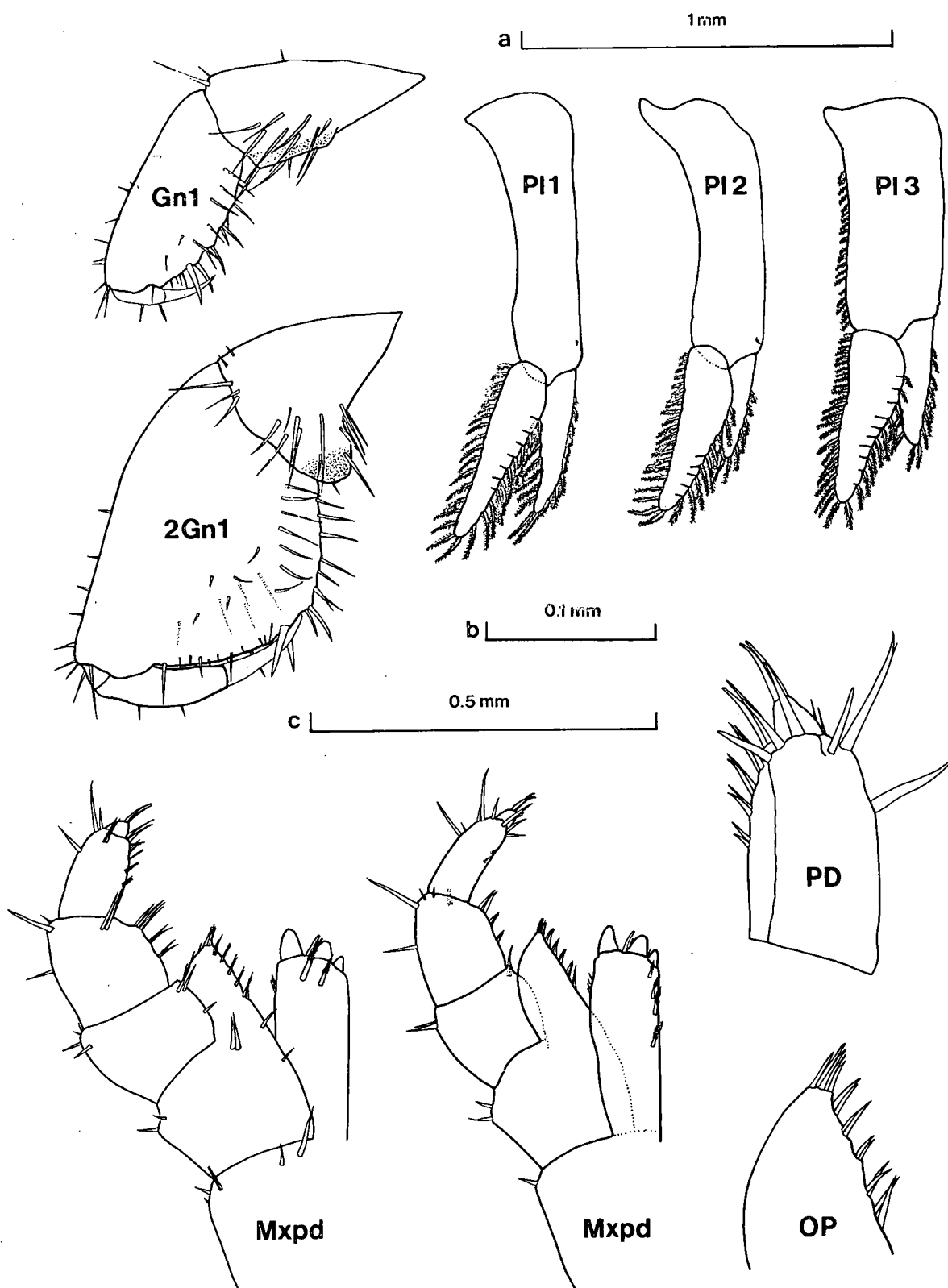


FIGURE 3.35 *Mysticotalitrus tasmaniae* (Ruffo) gen.n., ♀. 2, ♂.
Scale a; P11-3, Gn1, 2Gn1. Scale b; OP, PD. Scale c; Mxpd.

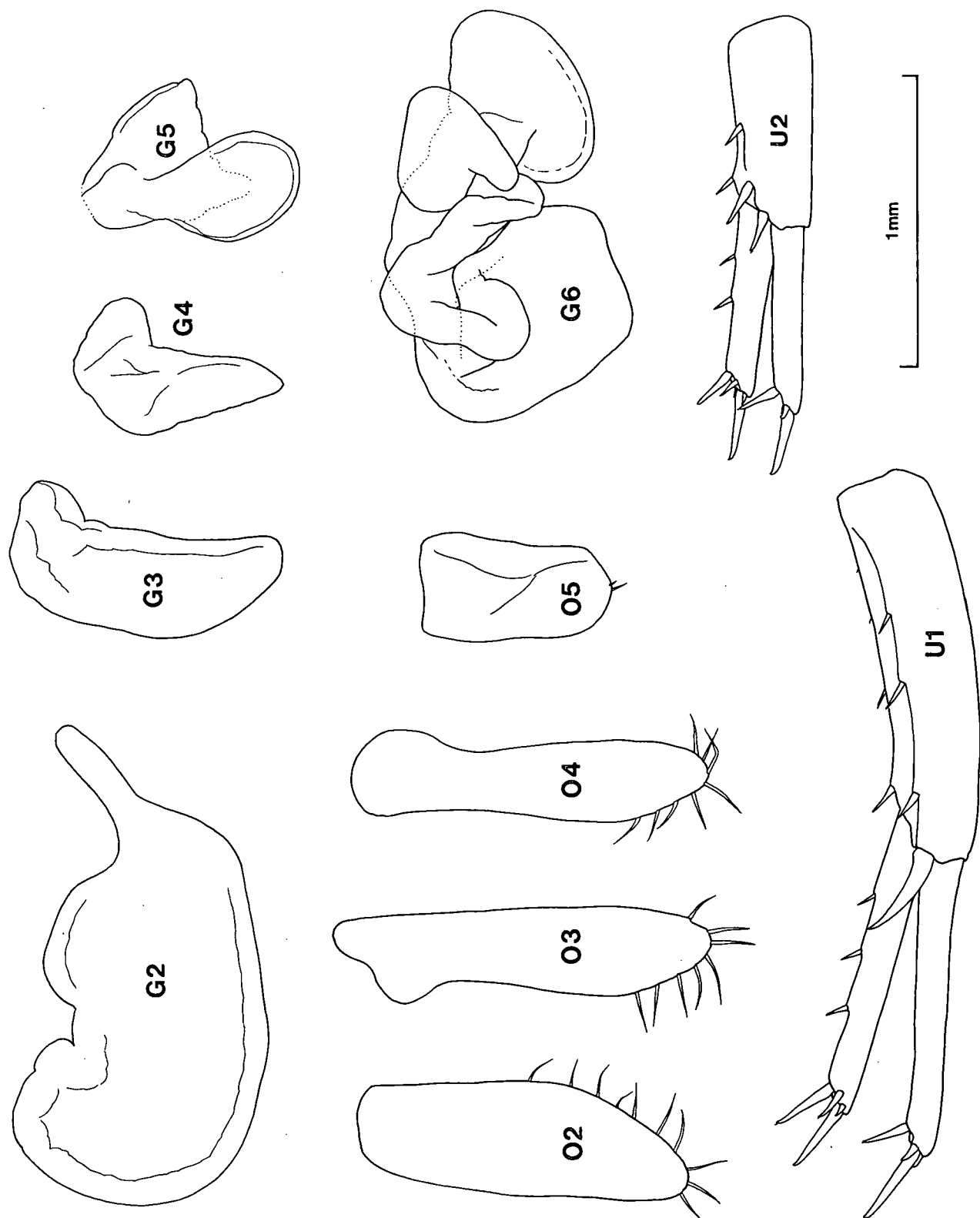


FIGURE 3.36 *Mysticotallitrus tasmaniae* (Ruffo) gen.n., ♀.

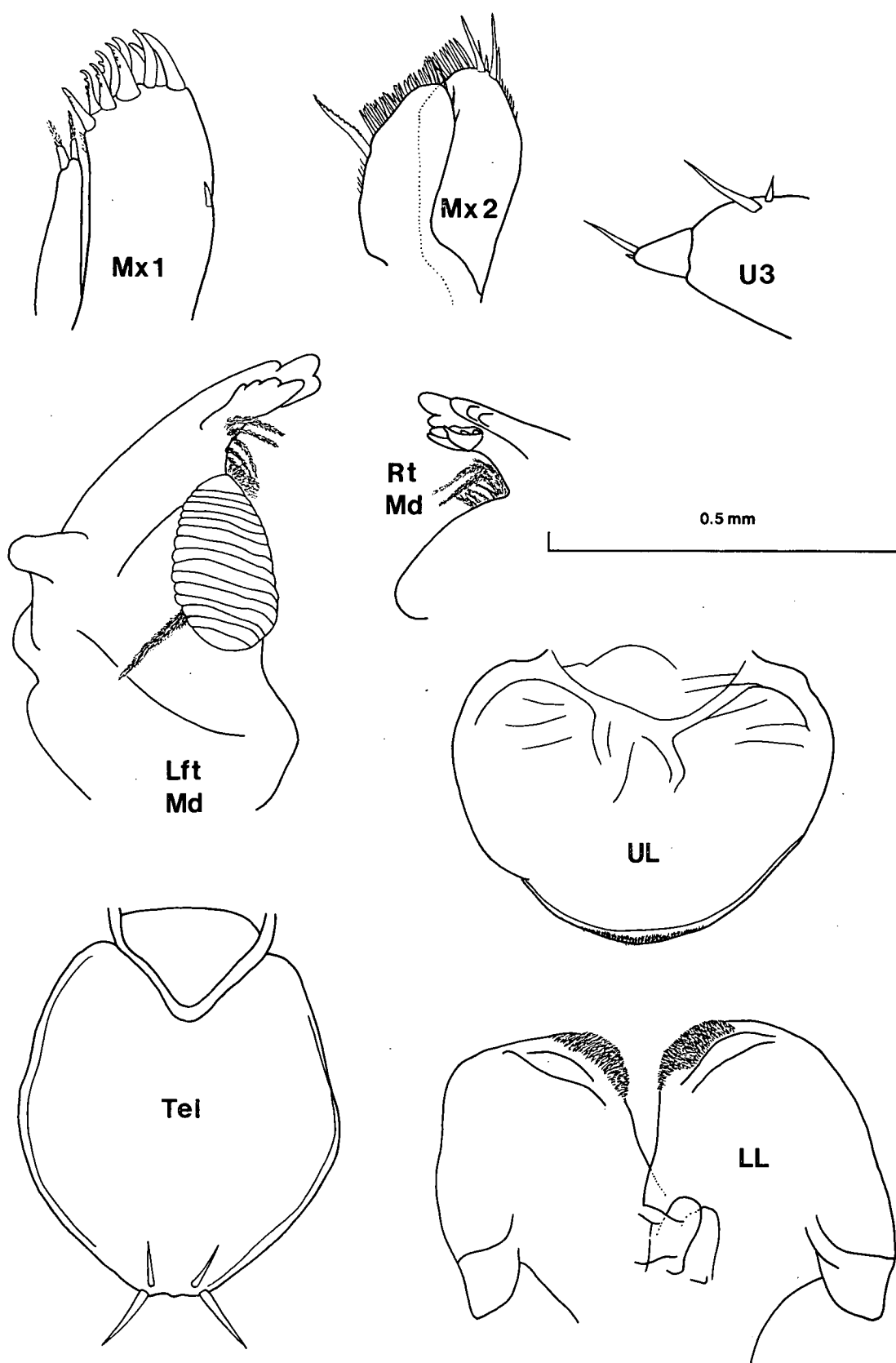


FIGURE 3.37 *Mysticotallitrus tasmaniae* (Ruffo) gen.n., ♀.

terminal spines on each ramus long, slender. Uropod 2, peduncle quite slender, with one inner and two outer marginal spines and an apical spine; rami subequal, shorter, outer bearing no marginal spines, inner with two. Uropod 3 small, peduncle short, with a long and a short spine; ramus very short, conical, bearing two unequal apical spines.

Telson broad, apex blunt, little trace of cleavage, one large and one small spine on each side of the apex.

Male:

Length 11.8 mm. Antenna 1 flagellum of 6 segments [3-6], second antenna with a 26-segmented flagellum [8-26].

Gnathopod 1, segment 2 strong, convex behind, segments 5 and 6 swollen to form a very powerful subchelate hand, segment 5 short, very deep, medially spinose with a prominent tumid lobe behind, segment 6 broadening distally, as long as segment 2, width two-thirds breadth, hind margin bearing a row of spines, a medial submarginal spine-row present; palm as long as hind margin, convex, bearing two strong spines between which the long, strong dactyl closes, dactyl not quite reaching end of palm, which ends at a distinct corner bearing two spines. Dactyl two-thirds as long as segment 6, terminal spine extremely strong, curved.

Otherwise similar to ♀, but bearing ventral penes on peraeonite 7 and lacking oöstegites.

Remarks

Hunt (1925) examined a female landhopper from Tasmania and provided drawings of the maxilliped palp, distal segments of gnathopod 1 and the second epimeral plate. In his opinion, this was an undescribed species which might belong to *Parorchestia* Stebbing. Hunt's drawings, particularly of the distinctive first gnathopod and second epimeral plate, leave no doubt that this was a specimen of *Mysticotalitrus tasmaniae*.

Ruffo's description of the species (1949) was based on two females, both with damage to the posterior end, which may account for his failure to notice the interramal spine of uropod 1. These specimens are in the collections of the Museo Civico di Storia Naturale at Genoa (Dr. L. Capocaccia, pers. comm.), but were not available for study.

The male of *M. tasmaniae* has not been described before. Mature males are smaller than females and possess the greatly enlarged hand of the first gnathopod which is also found in *Austrotroides maritimus* sp.n. and several species of *Keratroides* from the eastern Bass Strait islands, not dealt with here. In *M. tasmaniae*, this hand is used in male-male encounters and perhaps also in mating.

Specimens of *M. tasmaniae* found in all areas north of the Derwent R. (see Chapter 4) have gnathopod 1 less swollen in both sexes than those at the type locality.

Information on biology, population dynamics, and energy flow is contained in an unpublished Honours thesis at the Zoology Department, University of Tasmania (Friend, 1975).

Mysticotalitrus crypticus, sp.n.

Figures 3.38 - 3.41

Talitrus sylvaticus. Thomson 1893 (*partim*) p.59, pl.iv, figs. 8,9.

Types:

Holotype ♀ (ovig., 8 eggs); Near Brown's Rd., Fern Tree, Mt. Wellington, Tasmania. In litter in an area of eucalypt forest unburnt in 1967 fires, above Pipe Track. UGR 8312-197470. Coll. JAF 2.ii.1979 (8312-12). Allotype ♂; same data as holotype. Paratypes 12 ♂♂, 33 ♀♀ (16 ovig.), 2 imm.; same data as holotype.

Other material examined: TASMANIA:

3 ♂♂, 3 ♀♀ (1 ovig.), 3 imm., National Museum of Victoria, Melbourne; Kingston, leaf mould. Coll. C. Oke. 14.v.1948.

8012-5(3), -7(2), -8(9), -32(6), -33(1), -39(10), -60(1+)

8013-16(7), -18(26)

8110-5(3), -6(17), -11(20), -12(31), -14(10), -15(33), -16(25),
-21(2), -23(5), -24(9)

8112-1(3), 7(5)

8113-1(9), -15(12)

8210-3(10), -5(2), -7(2), -10(3), -15(2), -16(4), -18(5), -19(11)

8211-2(11), -3(3), -4(1), -5(4), -6(3), -7(1), -8(2), -10(2), -11(9),
-12(3), -13(3), -14(6), -15(8), -16(1), -18(4), -19(5), -20(3),
-21(5), -22(1), -23(7), -24(4), -25(1), -26(4), -29(2), -30(25), -31(2)

8212-2(1), -4(1), -5(6), -7(17), -11(1)

8311-1(2), -6(1)

8312-2(6), -3(6), -5(39), -6(3), -7(85), -8(20), -9(76), -14(1), -15(9)

8411-2(2), -6(1)

8412-1(4), -3(4), -6(8), -7(5), -8(2), -9(12), -10(3), -11(7), -12(22)
-16(23), -17(8)

8413-1(1), -2(3), -3(15), -4(1), -5(6), -10(8), -11(3), -12(3), -14(16)

-17(3), -19(1), -22(2), -23(13)

8512-1(17), -2(6), -3(5), -4(28), -5(35)

Diagnosis

A large landhopper of the genus *Mysticotalitrus*, with gnathopod 1 not swollen in animals of either sex, oöstegites with long slender setae, hind corners of epimeral plates 2 and 3 obtuse but sharp, and telson with two pairs of marginal spines as well as apical spines.

Description

Female:

Length 11.6 mm, ovigerous, with 8 eggs [1-8]. Head short, deeper than long, eye large, round, width almost half head length. Antenna 1 reaching one-third of the way along last peduncular segment, flagellum shorter than peduncle, composed of six segments [3-6]. Antenna 2 fairly long, as long as head and first four peraeon segments, peduncular segment 5 long, longer than rest of peduncle; flagellum longer than peduncle, [range of segment numbers in other specimens 8-17+] each segment long, bearing 4 groups of 3 slender setae. Upper lip broad, lightly pilose apically, indentation of right margin quite prominent. Lower lip broad, lateral lobes short, pilosity present on parts of inner shoulders only, central cleft margins bare. Left mandible, incisor 5-cusped, lacinia mobilis 4-dentate, molar 15-striate; right mandible, incisor with 5 cusps, lacinia 3-dentate. Maxilla 1, inner plate quite stout, short, apical setae short; outer plate broad, palp tiny, 2-segmented, terminal spine-teeth mostly long, slender, well separated, sparingly dentate, innermost spine-tooth leaning inwards, dentition formula 0-0-3-4-2-2-2-2-3. Maxilla 2 short, broad, outer plate wider and just longer than inner; inner plate inner margin pilose in parts, plumose seta large, distal spines short, strong, and fairly sparse; outer plate bearing a row of six spinules distally on outer margin, two long sharp spines near the broad apex, rest

of spine-row comprising fairly short sharp spines.

Maxilliped, inner plate broad, distally truncate, apex with two very large spine-teeth, two unequal small ones, and a stout blunt spine; two large submarginal plumes borne on the medial surface near inner margin. Outer plate shorter than inner plate and spine-teeth, outer margin arcuate, sharp apex bearing a group of six sharp spines; inner margin with two single spines and a group of three spines. Palp segments 2 and 3 with narrow lateral lobes, each with several pairs, or single inner marginal spines; segment 4 quite broad, prominent, bearing a large distal spine, not masked by lobe of segment 3; medial spines of segment 3 quite large.

Gnathopod 1, coxal plate deep, spinose below. Segment 2 slender, spinulose in front, broadening distally. Segment 5 longer than 6, with slender medial and posterior spines, posterior tumescence extremely shallow. Segment 6 sublinear, slender, hind margin gently convex, corrugated and spinose; posterior distal narrowing of segment hardly constituting a palm and greatly exceeded by stout dactyl with long slender terminal spine.

Gnathopod 2, coxal plate broad, posterior process almost a right angle, sharply rounded, lower margin smoothly curving and lightly spinulose. Gill large, broad proximally, anterior extension long and slender; oöstegite quite short bearing seven long, slender setae on apex and along anterior margin. Segment 2 long, broadening distally, front margin spinulose. Segments 3 and 4 subequal, 4 with a small tumid lobe behind. Segment 5 long and narrow, poorly spinose, with a very shallow, broad posterior lobe. Segment 6 long, linear, narrow, just longer than 5, medial spine-row of small spines, dactyl small and longitudinal, terminal lobe acutely rounded.

Peraeopod 3, coxal plate shallow, spinulose below, posterior process acutely rounded. Gill sac-like, more than half as long as segment 2; oöstegite slender, longer than that of gnathopod 2, bearing nine long setae near apex and along anterior margin. Segment 2 narrow proximally,

broadening distally, segments 4-6 quite slender, dactyl short, terminal spine long, almost straight.

Peraeopod 4 similar, but gill shorter, oöstegite bearing eight setae near the apex, segments 2, 4 and 5 shorter.

Peraeopod 5, anterior coxal lobe large, anterodistally oblique, straight and spinose, hind lobe much smaller, concave behind. Gill small, bilobate, oöstegite about two-thirds as long as those of peraeopods 3 and 4, thick, with gill-like texture, apically provided with three tiny setae. Segment 2 narrowing distally, hind margin slightly concave, serrulate. Dactyl slender, terminal spine long, just curved.

Peraeopod 6, anterior coxal lobe very shallow, posterior lobe narrow, distally rounded. Gill large, complex, folded and lobate. Segment 2 long-ovate, almost straight behind, minute distal lobe present. Segments 4-6 slender, dactyl long, slender, long terminal spine almost straight.

Peraeopod 7 the longest, coxal plate small, shallow. Segment 2 large, much expanded behind, hind margin serrulate, distal lobe prominent. Segments 4-6 long, quite slender. Dactyl elongate, slender; together with long, slightly curving dactyl, over two-fifths as long as segment 6.

First epimeral plate shallow, lower margin slightly oblique, hind corner sharp, hind margin serrulate. Second plate the deepest, front corner and lower margin one sweeping curve, hind corner sharp, obtuse, serrulate hind margin distally straight. Third plate, front corner more sharply rounded than second, more gently curving below; hind corner sharp, hind margin straight, serrulate.

Pleopods all reduced, biramous, setose, first longest, second and third subequal; peduncles progressively shorter and stouter posteriorly, all bearing two coupling spines; outer rami the longer, segmentation indistinct. Inner and outer rami of third pleopod respectively, intermediate in length between those of first (longer) and second pleopods.

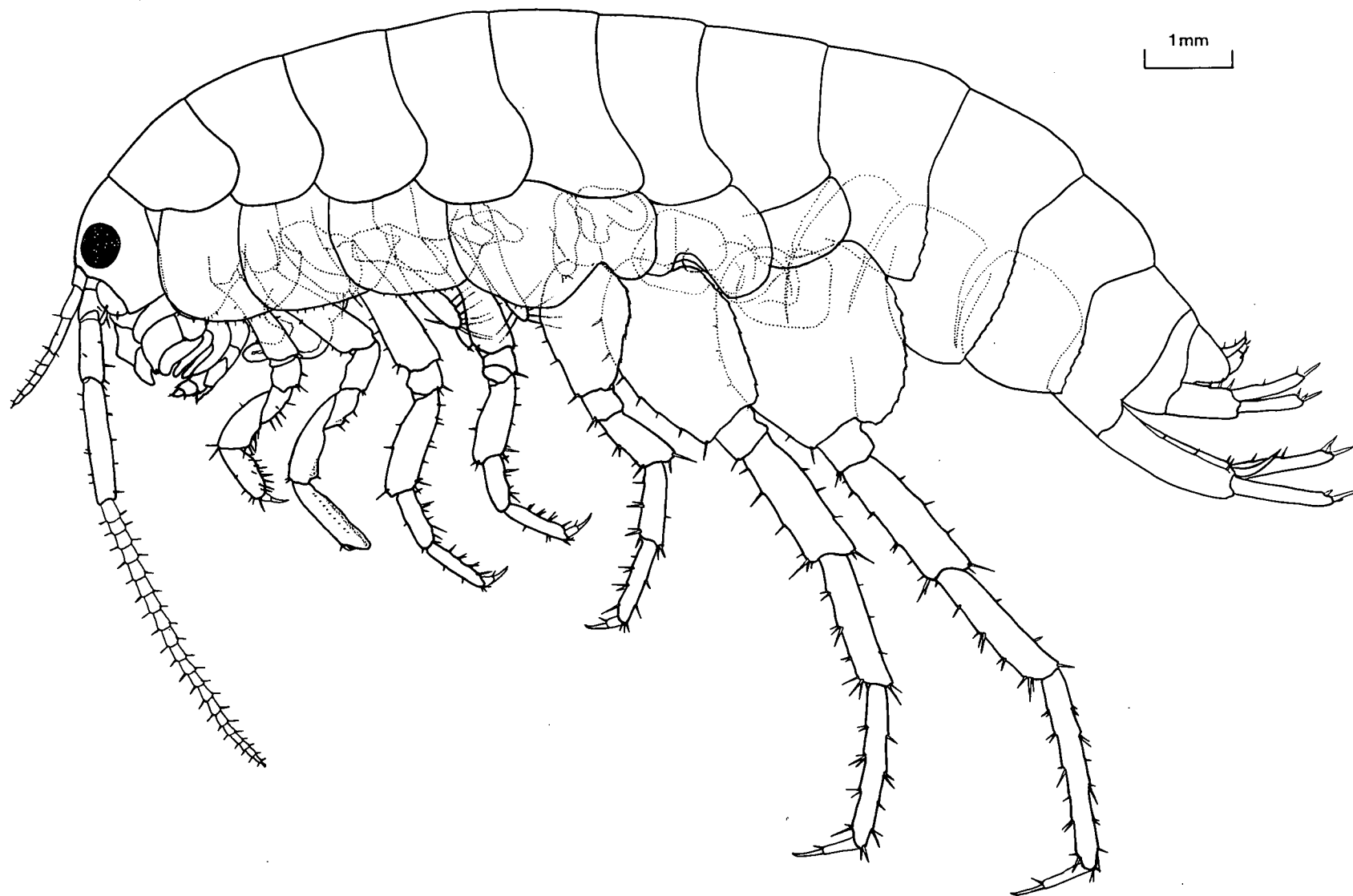


FIGURE 3.38 *Mysticotalitrus crypticus* gen. et sp.n., holotype ♀.

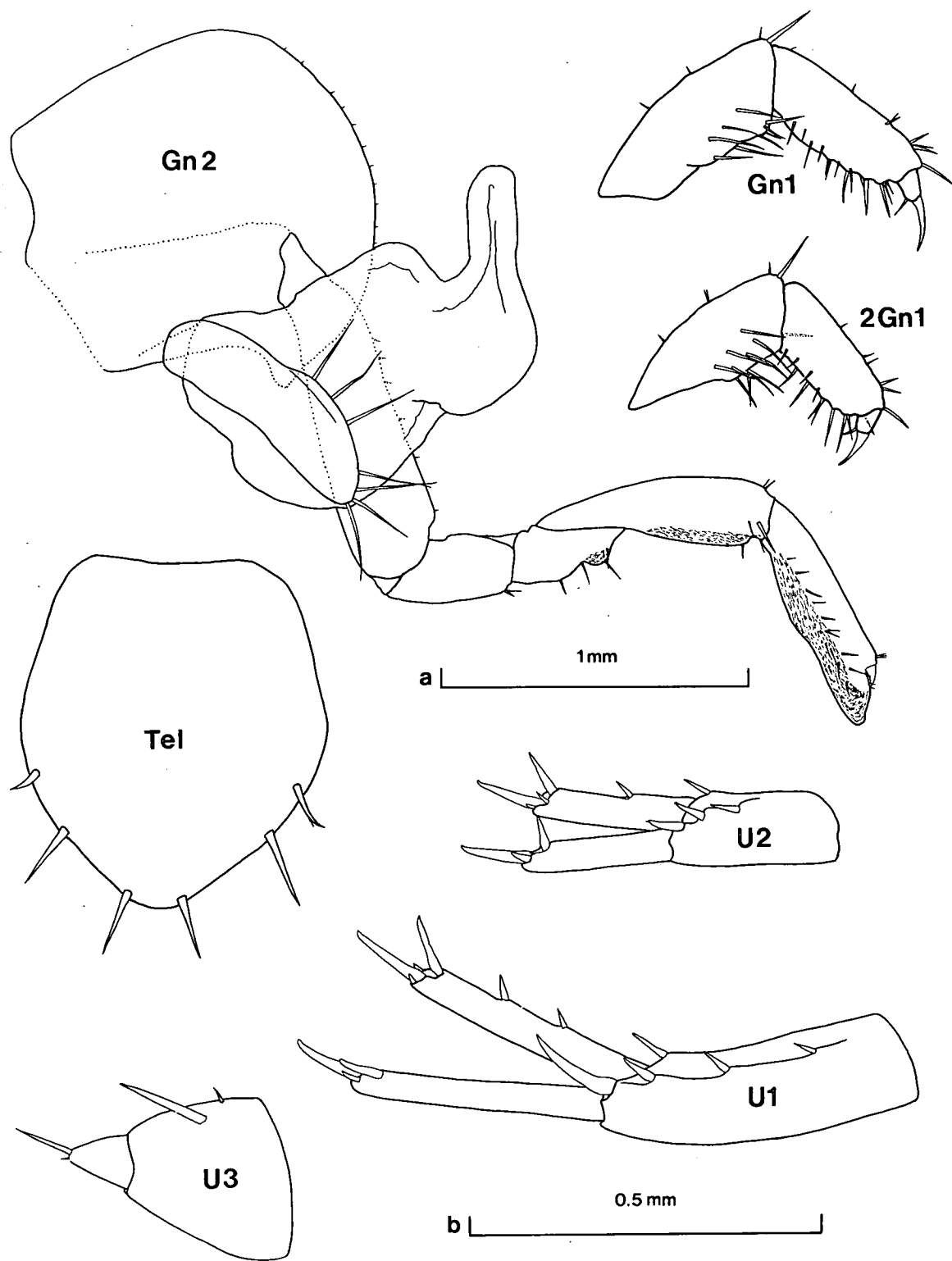


FIGURE 3.39 *Mysticotalitrus crypticus* gen. et sp.n., holotype ♀.
2, allotype ♂. Scale a; Gn1&2, 2Gn1, U1&2. Scale b; Tel, U3.

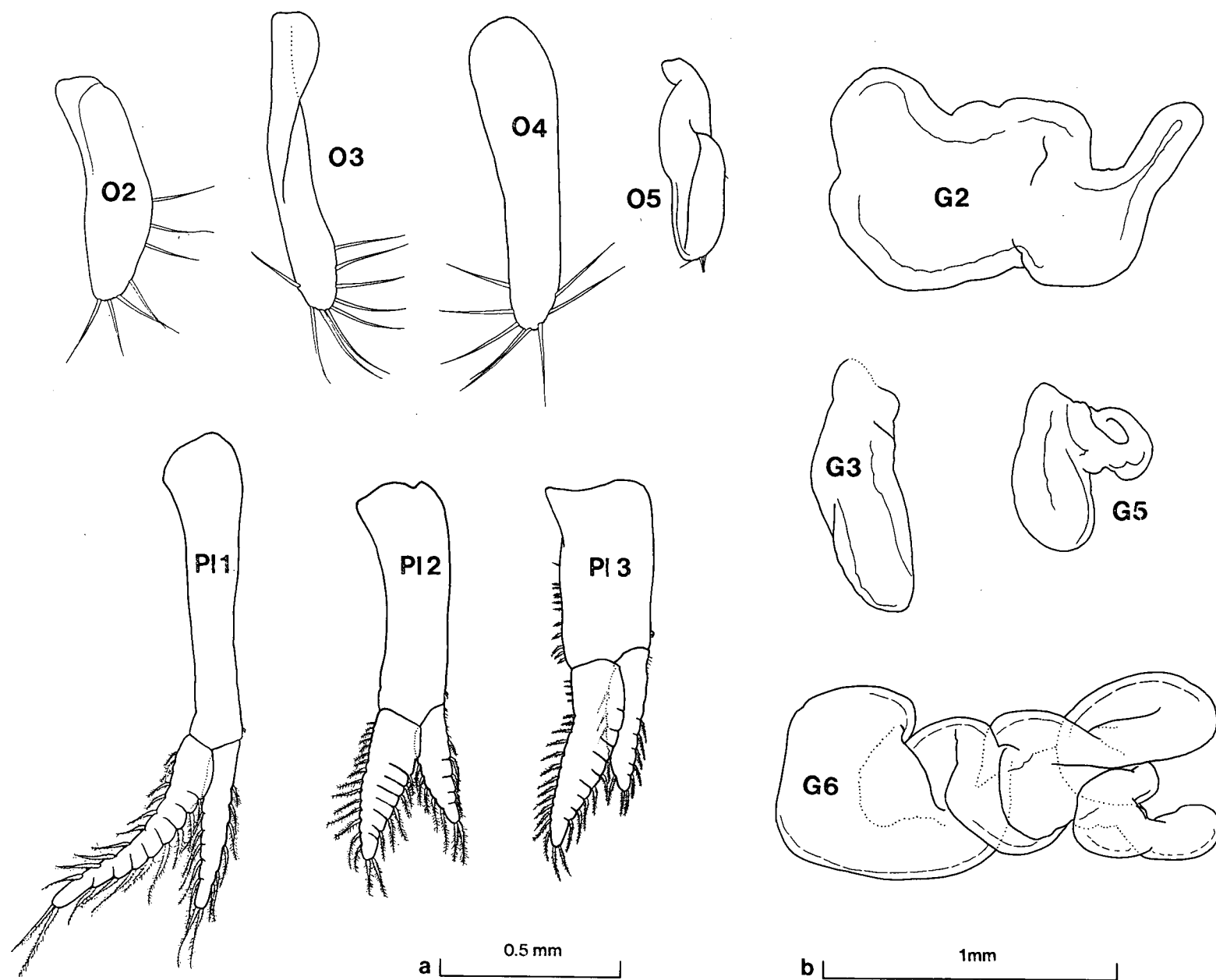


FIGURE 3.40 *Mysticotalitrus crypticus* gen. et sp.n., holotype ♀. Scale a; P11-3. Scale b; O2-5, G2,3,5,6.

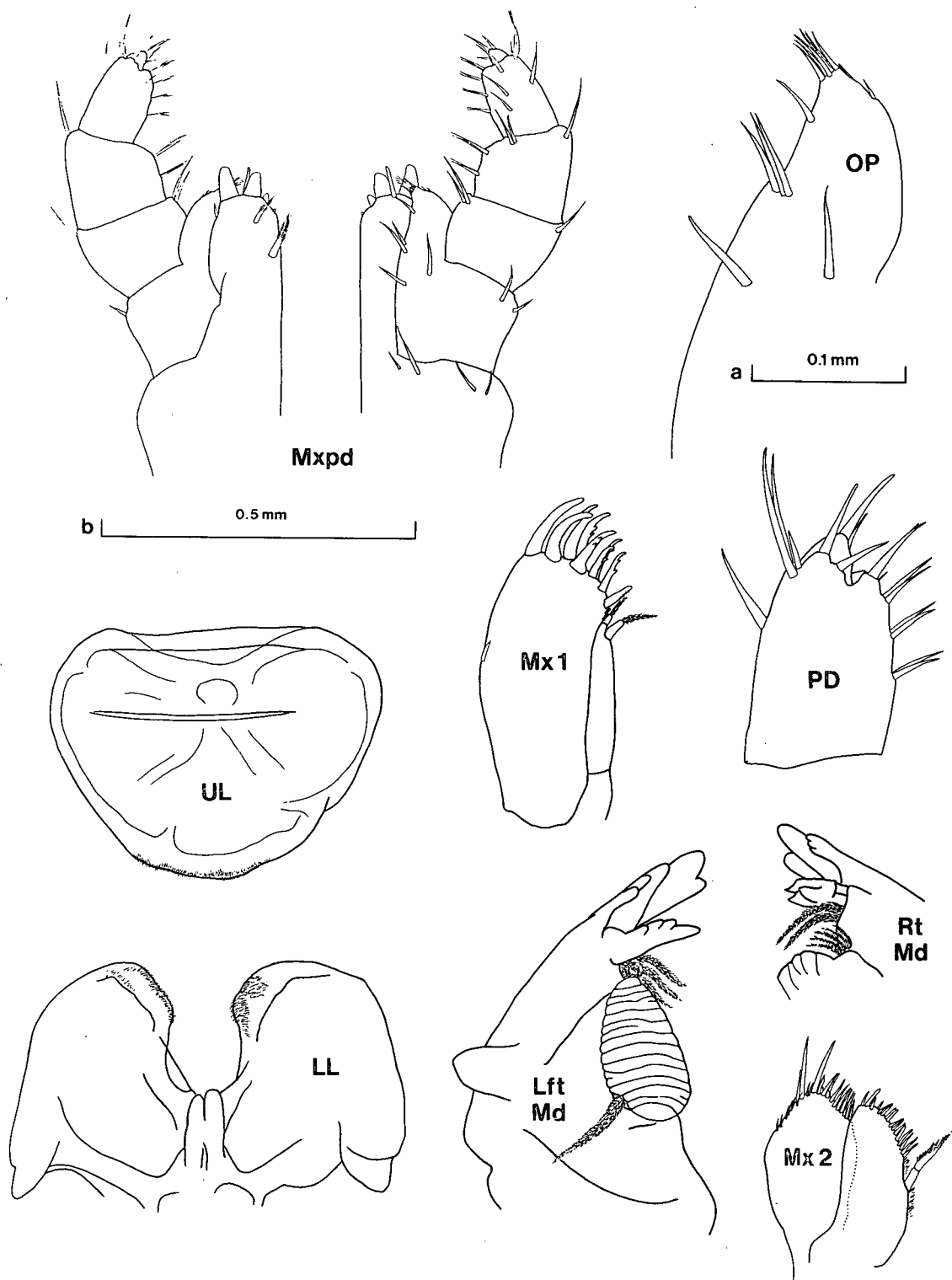


FIGURE 3.41 *Mysticotralitrus crypticus* gen. et sp.n., holotype ♀.
Scale a; OP, PD. Scale b; Mxpd, Mx1&2, UL, LL, Lft Md, Rt Md.

Marginal plumose setae small, peduncle of third pleopod bearing a row of tiny plumose setae on outer margin.

Uropod 1, peduncle bearing one inner and three outer marginal spines, apical spine strong and curved; rami subequal, shorter than peduncle, outer ramal margins bare, inner ramus with two marginal spines, apical spines long, longitudinal. Uropod 2, peduncle just longer than rami, bearing one inner marginal spine, three outer (one apical); rami subequal, outer ramus with margins bare, inner ramus bearing one spine halfway along; apical spines long, one on each ramus longitudinal, almost half ramal length. Uropod 3, peduncle short, stout, bearing one large spine and a spinule; ramus short, conical, with two unequal spines on the apex.

Telson broad, apex entire and gently rounded, one apical spine and two marginal spines on each side.

Male:

Length 7.6 mm. Antenna 1 flagellar segment number 5 [3-6], that of antenna 2, 16 [8-20+]. Otherwise like ♀, but bearing paired penes ventrally on peraeonite 7 and lacking oöstegites.

Remarks

M. crypticus sp.n. is very close to *M. tasmaniae*, but is distinguished from it by its second and third epimeral plates, which both have the hind corner sharp, not rounded as in *M. tasmaniae*, and by its telson which has marginal spines as well as the apical spines found in the other species. *M. crypticus* sp.n. lacks the distally swollen first gnathopod of *M. tasmaniae*, although this difference is hard to detect in immature specimens and in the northern part of the range of *M. tasmaniae*.

It is obvious that Thomson (1893) had at least two species in his collection from the Springs, on Mt. Wellington. The gills which he described belong to a *Mysticotalitrus* species. His illustrations of the

first pleopod and telson agree with those given here for *M. crypticus* sp.n., while most of the other parts drawn belong to *Keratroides vulgaris* (Friend) (q.v.). The second gnathopod drawn by Thomson (Figure 6) could belong to a number of species, including the three species found today on Mt. Wellington, *M. crypticus* sp.n., *M. tasmaniae* and *K. vulgaris*.

Females of this species are larger than males and carry up to 8 eggs. The reference in Friend (1979) to a female landhopper with a sperm mass held against the ventral surface beneath the reduced oöstegites of peraeopod 5 was to an individual of *M. crypticus* sp.n. The specific name is an allusion to the ease with which an individual of this species is hidden amongst a collection of *M. tasmaniae*.

Genus *Arcitalitrus* Hurley 1975 (~~stat. nov.~~)

Talitrus (*Arcitalitrus*) Hurley, 1975a, p.161

Diagnosis

Large, apomorphic landhoppers with sexually similar gnathopods, characterised by the following: maxilliped outer plate arcuate, acute apex bearing a group of spines; hand of gnathopod 1 simple, segment 6 long, narrowing distally, that of gnathopod 2 mitten-like, apical lobe sharp; epimeral plate 2 rounded below, hind corner sharp, hind margin straight, epimeral plate 3 subsquare, rounded in front, convex below, hind corner sharp.

Other features include: maxilliped palp slender, lateral lobes narrow, fourth segment unmasked; oöstegites short, slender, with apical setae only; anterior and posterior gills much larger than others, peraeopod 6 gill anseriform; pleopods variously normal, reduced or vestigial; uropods 1 and 2 sexually similar, outer rami lacking marginal spines; uropod 3 small, ramus very short, apical spines only; telson entire.

Type species: *Arcitalitrus sylvaticus* (Haswell).

Distribution: Queensland, N.S.W., Victoria; introduced to California.

Other species: *A. dorrieni* (Hunt)

Distribution: Queensland, N.S.W.; introduced to New Zealand, Norfolk I., Isles of Scilly, Ireland, Cornwall.

A. sp. S (diagnosis below).

Remarks

Arcitalitrus was originally founded by Hurley (1975a) as a monotypic subgenus to receive *Talitrus sylvaticus* Haswell, characterised by its arcuate maxilliped outer plate. At least eight species in eastern Australia possess this distinctive maxilliped form, and one of these species (diagnosed below) is found in Tasmania.

The group, recognized here at the generic level, displays a number of apomorphic features, including the slender, poorly spinose maxilliped palp, specialised outer plate, enlarged anterior and posterior gills, small oöstegites with apical setae only, reduced pleopods and small third uropods. It includes *Arcitalitrus dorrieni* (Hunt) which is similar to but distinct from *A. sylvaticus*, from which it differs in possessing well-developed first and second pleopods with equal rami and long plumose setae fringing the outer peduncular margins, apically cleft peraeopod 6 gills and epimeral plate 2 much longer than plate 3.

Figure 3.1.

Talitrus sylvaticus. Chevreux, 1901, p.392, figure 7.

Material examined: TASMANIA:

7719-1(12), -3(35)

7816-7(12), -8(11), -9(14), -10(28), -11(9), -22(3)

7817-1(13)

7818-1(19), -3(3)

VICTORIA: 5 specimens, Australian Museum; Mt. Donna Buang, 1060 m, wet sclerophyll. ANIC berlesate 299, coll. RWT & RJB, 5.xi.1970. 2 specimens, Australian Museum; Mt. Arnold Rd., E. Marysville, wet sclerophyll, 600 m. ANIC berlesate 301, coll. RWT & RJB, 4.xi.1970. 3 specimens, Australian Museum; Cement Ck., 5 km N of Warburton, leaf/log litter. ANIC berlesate 591, coll. JL & TW, 19.i.1978. 34 specimens, Australian Museum; Cement Ck., 5 km W of Warburton, leaf and log litter. ANIC berlesate 592, coll. JL & TW, 19.i.1978. 21 specimens, Australian Museum; Cumberland Ck. 13 km ESE of Marysville, leaf and log litter. ANIC berlesate 593, coll. JL & TW, 18.i.1978. 39 specimens; Nr. picnic area 11 km E of Nelson (W of Mt. Richmond N.P.). Coll. JAF, xii.1975. 11 specimens; 3 km N of Peterborough, low eucalypt scrub, under leaf litter and bracken on sandy soil, quite dry. Coll. JAF, xii.1975. 9 specimens; Under stones near W shore of L. Purrumbete, nr. Camperdown. Coll. PSL, 26.ix.1977. 1 specimen; Snobs Ck. above falls. Eucalypt regrowth. Coll. AMMR, 17.v.1979. 3 specimens, National Museum of Victoria; Cement Ck., Mt. Donna Buang. Coll. A. Neboiss, April, 1976.

Diagnosis

A large landhopper of the genus *Arcitalitrus* with sexually similar gnathopods, peraeopod gill elongate, anseriform, subdistally broadly incised, distally narrowing to a subacute apex, and pleopods all biramous and setose, progressively smaller posteriorly with outer rami just longer

than inner rami.

Remarks

This undescribed landhopper species has been found in one locality in northwest Tasmania (also on Hunter, Robbins and King Is. to the northwest), and is the only mainland Australian species so far found on the island of Tasmania (see Chapter 4). These specimens are morphologically very similar to Victorian material examined. A full description and drawings are not included here because this species is being treated in other work in progress.

The drawing of the first pleopod of an Australian amphipod by Chevreux (1901) very closely resembles that appendage in *Arcitalitrus* sp.S; Chevreux noted that the specimens, sent to him by Chilton, had all pleopods biramous, with the third pair smaller than the first and second pairs, as in this species. Chilton (1916) pointed out that the specimens he sent Chevreux were from Mt. Kosciusko, which is in the Snowy Mts. in New South Wales, near the Victorian border.

Genus *Keratroides* Hurley 1975 (~~stat. nov.~~)*Talitrus* (*Keratroides*) Hurley 1975a p.162*Talitrus* (*Keratroides*) Friend 1979 p.95

Diagnosis

Apomorphic, sexually similar landhoppers characterised by distally truncate maxilliped outer plate, bearing spine-groups at each corner (except in *K. albus* sp.n.), gnathopod 1 non-palmate, hand of gnathopod 2 mitten-shaped, lack of oöstegite on gnathopod 2, peraeopod 6 gills large and anseriform, pleopods reduced, usually vestigial, epimeral plate 3 with distal margin concave, uropod 3 very small and telson distally broad and marginally spinose. Other features include short antenna 1, broad, shallow upper and lower lips, maxilla 1 broad, spine-teeth strong, innermost almost lateral, maxilla 2, inner plate spines short, strong and well-separated; maxilliped inner plate poorly setose, outer plate palp slender, lateral lobes vestigial or absent; gnathopod 1 distal segments short, strong, segment 6 proximally expanded, gnathopod 2, segment 2 anterior margin bearing several long spines, distal segments short, strong, segment 2 proximally expanded; anterior and posterior gills large, others small, lobate; pleopod 3 reduced to a vestigial stump, uropods 1 and 2 with margins of outer ramus bare, peduncular apical spine of uropod 1 strong and simple, uropod 3 ramus with no lateral spines.

Type species: *Keratroides kershawi* (Sayce)

Distribution: Victoria

Other species: *K. vulgaris* (Friend)

Distribution: Tasmania

K. angulosus (Friend)

Distribution: Tasmania

K. albus sp.n.*K. rex* sp.n.*K. pyrensis* sp.n.

Remarks

Hurley (1975a) thought the morphology of the Victorian species *Talitrus kershawi* Sayce distinctive enough to warrant separation from the other landhoppers, placing it in a monotypic subgenus, *Talitrus* (*Keratroides*). Two new Tasmanian species were placed into Hurley's subgenus by Friend (1979) who slightly expanded the definition of the taxon.

Keratroides is a large group of apomorphic landhoppers which includes at least fifteen species from Tasmania, the Bass Strait islands and Victoria, and which is raised here to generic status.

Its component species share the features listed by Friend (1979) (which is expanded above) except that the pleopods are usually, but not always vestigial (i.e. in *K. albus* sp.n.). This diagnosis disagrees with Hurley's original definition on the following points:

maxilliped outer plate distally truncate, with a spine group at each of the two corners;

pleopods 1 and 2 reduced or vestigial, pleopod 3 a vestigial stump;

epimeral plate 3 distally slightly or strongly concave;

telson with 2-6 marginal spines.

Apomorphic features of the genus include the strong, simple first gnathopod and slender mitten-shaped second gnathopod in both sexes, the poorly spinose, narrow maxilliped palp and distally modified outer plate, the short, broad upper and lower lips and maxillae, the narrow oöstegites bearing apical setae only, the absence of an oöstegite on gnathopod 2, large anterior and posterior gills, and modified epimeral plates.

Keratroides is most closely related to *Arcitalitrus* which it resembles in the form of antennae, mouthparts, gnathopods, peraeopods, uropods and telson. *Keratroides* may be distinguished from *Arcitalitrus*

by its possession of a truncate maxilliped outer plate with two distal spine-groups, epimeral plate 3 distally concave and its lack of an oöstegite on ♀ gnathopod 1.

Keratroides superficially resembles *Austrotroides* in its tendency for pleopods to be vestigial and its simple first gnathopods. However, these genera are not closely related and may be distinguished from each other by the following features:

<i>Keratroides</i>	<i>Austrotroides</i>
Antenna 1 just exceeding penultimate segment of antenna 2 peduncle.	Antenna 1 reaching over $\frac{1}{2}$ -way along last segment of antenna 2 peduncle.
Maxilliped outer plate distally truncate, with 2 apical spine-groups (except in <i>K. albus</i> sp.n.).	Maxilliped outer plate distally rounded, with a submarginal spine-row or group.
Palp poorly spinose, lateral lobes vestigial, fourth segment obvious.	Palp spinose, lateral lobes well-developed, fourth segment masked.
Maxillae short and broad, maxilla 1 inner spines leaning inward.	Maxillae long, narrow, maxilla 1 spines parallel, longitudinally oriented.
Hand of gnathopod 1 short, proximally broad, lacking any palm (except in <i>K. albus</i> sp.n.).	Hand of gnathopod 1 long, slender, with a short, oblique palm.
♀ gnathopod 2 lacking oöstegite.	♀ gnathopod 2 with oöstegite.
Uropod 3 very small, ramus short, without lateral spines.	Uropod 3 relatively long, slender, ramus elongate, usually with lateral spines.
Telson large, entire, with several marginal spines each side.	Telson small, apically cleft, with one or no marginal spines each side.

Keratroides albus, sp.n.

Figures 3.42 - 3.46

Types:

Holotype ♀; APPM reserve, West Downs, nr. Surrey Hills, NW Tasmania. In distinct burrows in clay, beneath logs in *Nothofagus* forest. UGR 8015-863229. Coll. AMMR, 16.xii.1978 (8015-20). Allotype ♂; same data as holotype. Paratypes 3 ♂♂, 9 ♀♀ (1 ovig.), 4 imm.; same data as holotype.

Other material examined: TASMANIA:

7913-11(3)

7914-4(1), -5(2), -9(2)

7915-3(3), -4(1), -7(5), -9(1), -10(3), -12(1), -21(25)

8012-23(1), -24(3), -25(2), -29(2), -30(10), -31(3), -34(1)

-50(2), -51(9), -52(7), -65(1)

8013-15(4), -38(4), -39(3)

8014-14(1)

8015-2(5), -11(2), -13(2), -15(3), -21(6)

8112-12(1)

Diagnosis

A large, very distinctive unpigmented landhopper with short antennae, rounded head, small eyes, shallow body and heavy appendages, adapted for burrowing in the soil of wet forests.

Description

Female:

Length 12.5 mm, with no eggs [4]. Head as long as deep, dorsal surface strongly rounded. Eye small and round, width about one-fifth head length. Antenna 1 very short, reaching just past distal end of penultimate peduncular segment of antenna 2; flagellum of 4 segments, [3-4], shorter than head and first three peraeon segments, shorter than

peduncle. Antenna 2 short, flagellum of 13 segments [7-14], most bearing four groups of two long spines; peduncle shorter than flagellum, distal segment short, no longer than penultimate two segments together.

Upper lip broad, shallow, apically pilose; lower lip, lobes broad, inner shoulders pilose, sides of central trough lightly pilose. Left mandible, incisor elongate, 4-cusped, lacinia mobilis 3-cusped, molar process well-developed, triturating surface with 20 ridges, anterodistal margin raised; right mandible, incisor broad, blade-like, 4-cusped, lacinia with a single cusp.

Maxilla 1, inner plate short, inner margin lightly pilose, apical plumose setae large; outer plate not narrowing distally, apical spines simple or poorly dentate, inner spines leaning inwards, innermost almost laterally oriented, dentition formula 0-0-0-3-3-2-1-2-1; palp slender, small, set proximally of midpoint, inner margin pilose. Maxilla 2, inner plate narrow, about half width of outer plate, apical spines relatively sparse, stout and sharp, plumose seta strong; outer plate lacking large spines near apex, outer margin pilose, spinose distally, rest of spine-row comprising well-separated, slender spines.

Maxilliped, inner plate bearing three subterminal plumose spines on the medial surface, three on the lateral surface, with two on the inner margin; three terminal teeth, inner very small, outer two tall, all with inner margin concave. Outer plate slender, narrowing distally to a small rounded apical projection obscured by subterminal group of spines. Palp very slender, bearing a few long spines, lateral lobes of segments 2 and 3 absent, segment 4 bearing two apical spines and delimited proximally by a slight shoulder.

Gnathopod 1, coxal plate broad and very shallow. Segment 2 stout, broadening distally with several spines on the anterior margin. Segment 3 broader than long, shorter than 4, which bears a very small posterior lobe. Segment 5 longer than 6, expanded posteriorly into a short scabrous lobe. Segment 6 small, subrectangular, posterior margin bearing few spines.

Short straight palm defined by two very stout spines between which the dactyl closes, with another stout spine midway along the palm. Dactyl strong, three-quarters the length of segment 6, greatly exceeding palm, terminal spine curved.

Gnathopod 2, coxal plate shallow, distal margin gently rounded, posterior process small, sharply rounded. Gill large, anterior extension long and broad, oostegite absent. Segment 2 slender, anterior margin spinose, slightly concave; segment 4 bearing a large posterodistal tumid lobe. Segment 5 as long as 6, distally spinose, hind margin deeply expanded into a broad scabrous lobe. Segment 6 long, posterior swelling distal, lobe elongate, fairly sharp; medial spine-row composed of numerous small spines, dactyl small.

Peraeopod 3, coxal plate small, very shallow, slight corner in front, posterior process bluntly rounded. Gill very small, sac-like but twisted, oostegite very slender, apically bearing three slender setae. Segment 2 strong, segments 4 to 6 bearing long spines behind; dactyl slender, terminal spine long, together well over half the length of segment 6.

Peraeopod 4 similar, but coxal plate smaller, posterior process smaller, acute, oostegite with four apical setae, segment 2 shorter.

Peraeopod 5, anterior coxal lobe very shallow, smoothly rounded in front and below, hind lobe small, straight posteriorly. Gill small, bilobate, oostegite two-thirds as long as anterior pairs, fleshy, with a spinule and some pilosity on the broad apex. Segment 2 narrowing distally, segments 4 and 5 short, heavy; dactyl long, slender, terminal spine very long, curved; whole segment three-quarters length of segment 6.

Peraeopod 6, coxal plate small, both lobes shallow. Gill large, anseriform; proximally lobate and very broad, posterior margin distally strongly indented near "head", terminally subacute. Segment 2 subovate, narrowing distally, hind margin almost straight, serrulate. Segments 4-6 strong, spines long; dactyl very long, slender, half as long as segment 6.

Peraeopod 7, coxal plate very shallow. Segment 2 broadly sub-ovate, weakly spinulose and serrulate behind, distal lobe very shallow. Segments 4-6 strong, spinose. Dactyl very long and slender, half as long as segment 6, terminal spine almost straight.

First epimeral plate very shallow, lower margin almost horizontal, hind corner sharp, hind margin gently convex. Second and third epimeral plates rounded in front, lower margin posteriorly concave, hind corner slightly produced behind, hind margin sinuous, lightly spinulose.

First pleopod reduced, biramous, peduncle almost as broad as long, inner margin expanded proximally, pilose, bearing two coupling spines; outer ramus the longer, shorter than peduncle, six-segmented, inner broader, segmentation indistinct; both rami bearing strong plumose setae marginally, apical setae very long. Second pleopod shorter, peduncle much narrower, but also expanded proximally on inner side, bearing four coupling spines, both margins pilose; outer margin with a plumose seta distally; only one ramus present, shorter and narrower than peduncle, segmentation indistinct, terminal setae long. Third pleopod a subrectangular stump, shorter than peduncle of second, rami absent, one subapical coupling spine present.

Uropod 1 quite short, peduncle longer than rami, bearing three outer and three inner marginal spines, apical spine straight and slender; outer rami just longer than inner, margins bare, one apical spine as long as peduncular apical spine; inner ramus bearing a marginal spine. Uropod 2 peduncle longer than rami, two outer and one inner marginal spine; rami subequal, inner strong, bearing the only marginal spine. Uropod 3 very short, peduncle as broad as long, with one long and two very small spines; ramus broader than long, with a small subapical spine.

Telson broad, entire, with 2-3 marginal spines and an apical spine on each side.

Male:

Length 12.5 mm. Antenna 1 flagellum of 4 segments [3-4], antenna

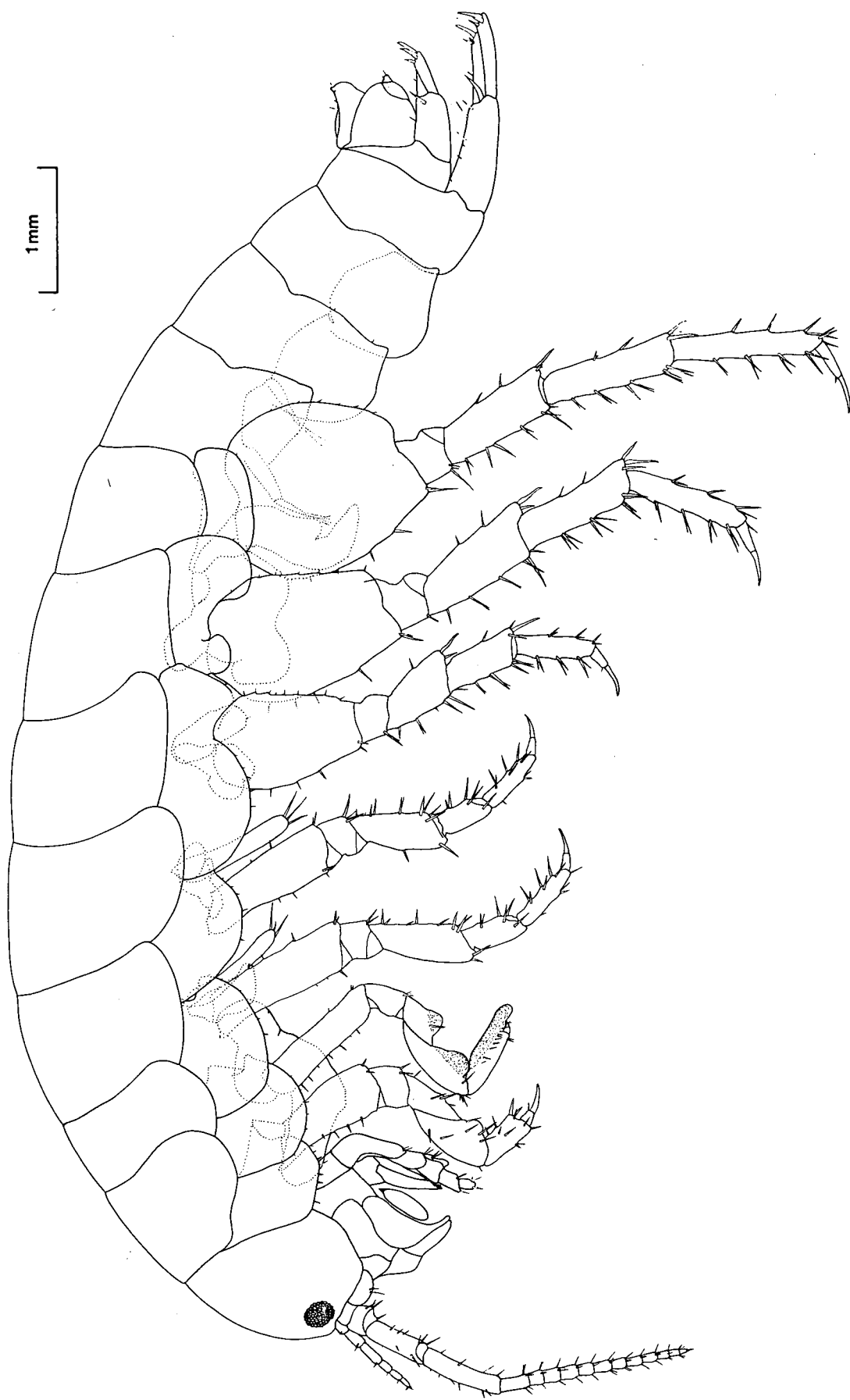


FIGURE 3.42 *Keratroides albus* gen. et sp.n., holotype ♀.

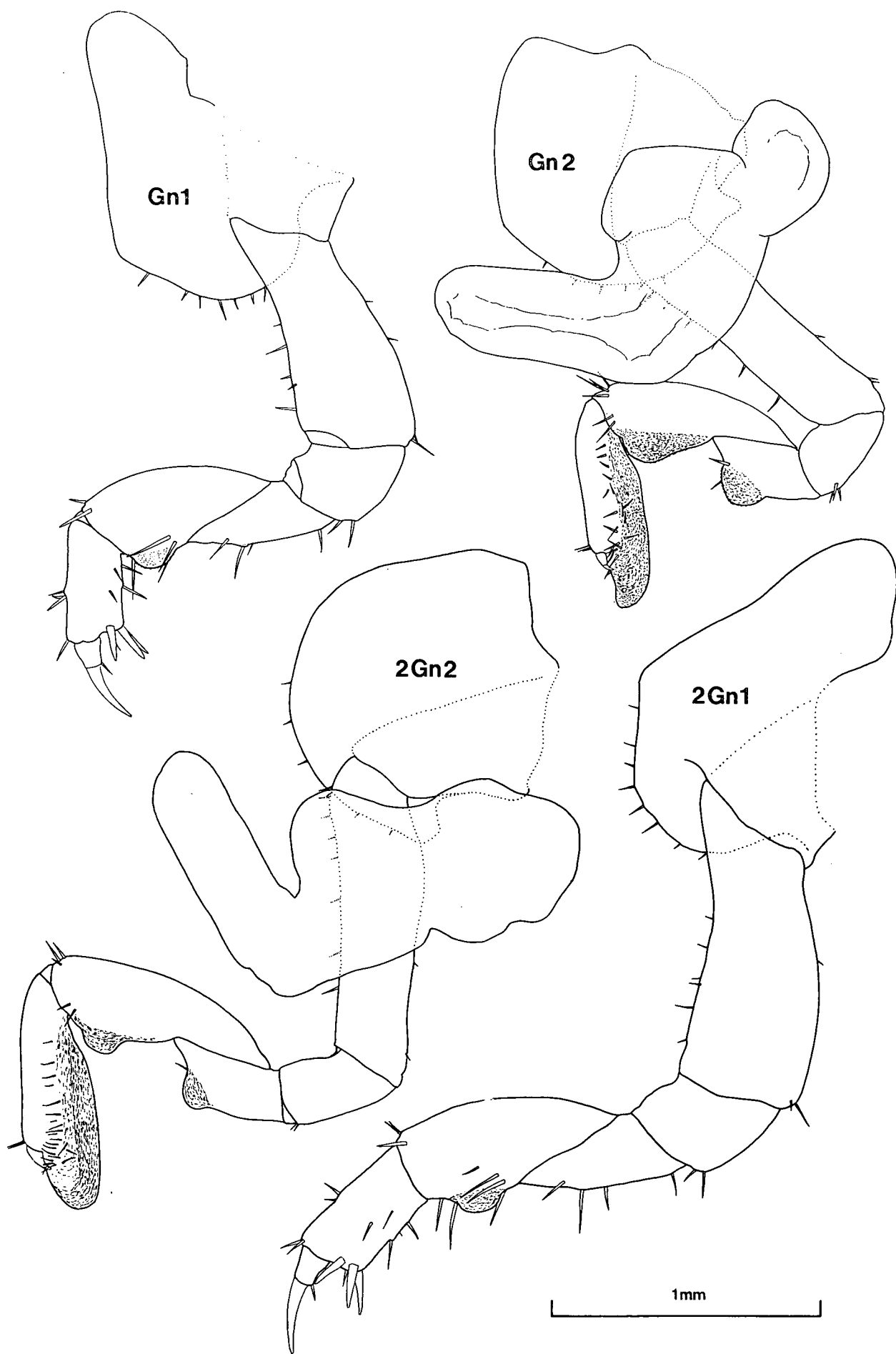


FIGURE 3.43 *Keratroides albus* gen. et sp.n., holotype ♀. 2, allotype ♂.

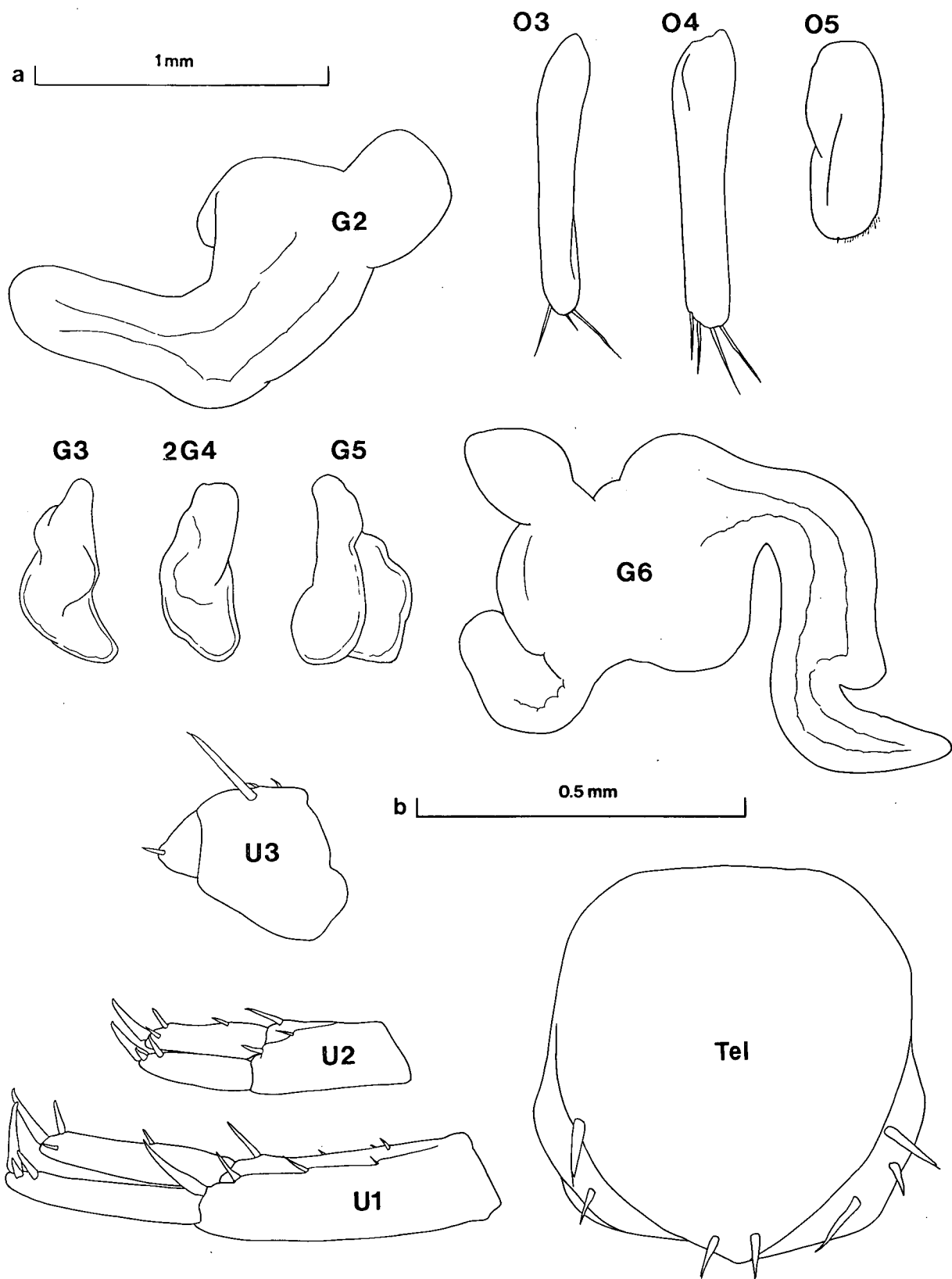


FIGURE 3.44 *Keratroides albus* gen. et sp.n., holotype ♀. 2, allotype ♂.
Scale a; G2,3,5,6, 2G4, O3-5, U1&2. Scale b; Tel, U3.

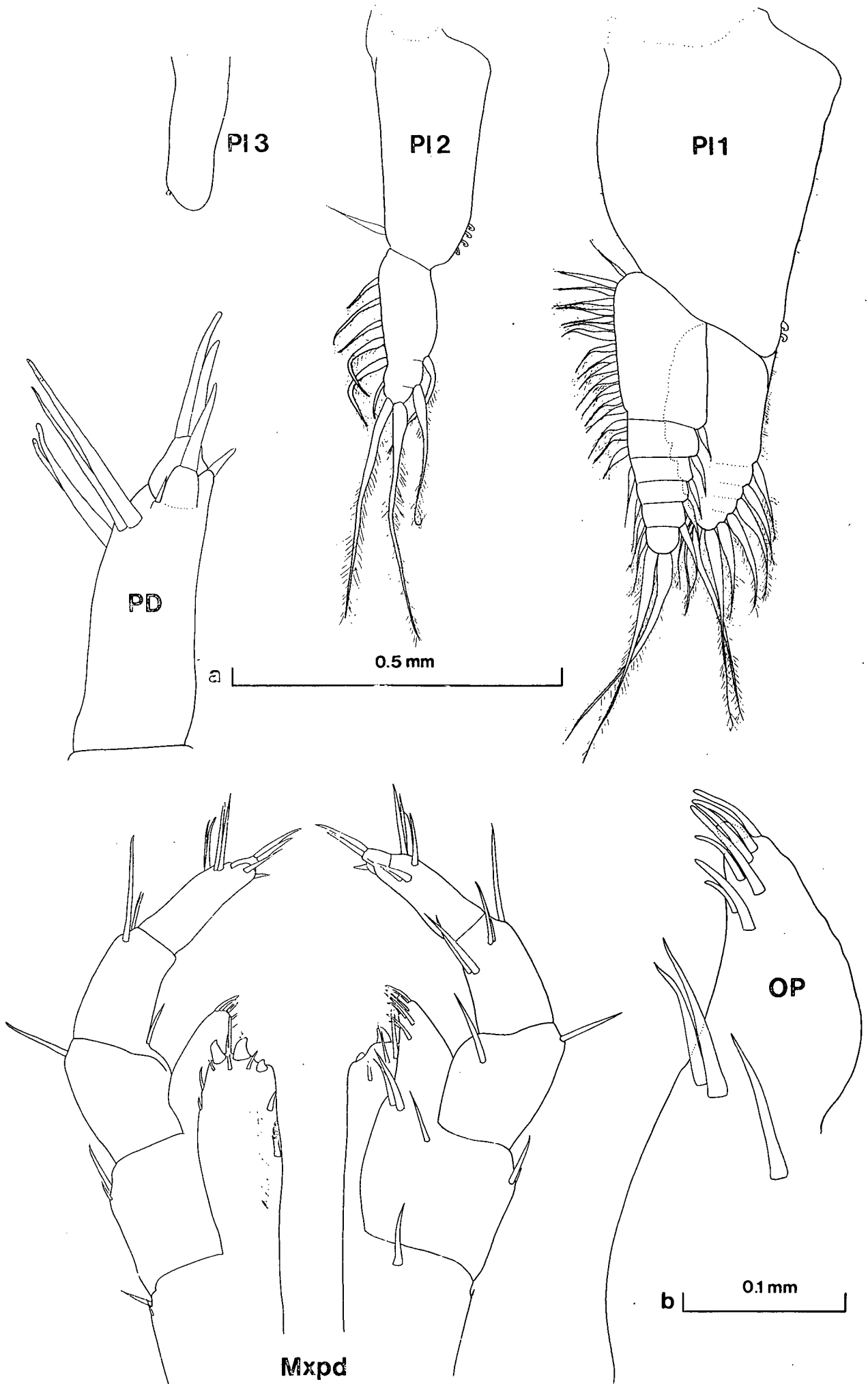


FIGURE 3.45 *Keratroides albus* gen. et sp.n., holotype ♀. Scale a; PI1-3, Mxpd. Scale b; OP, PD.

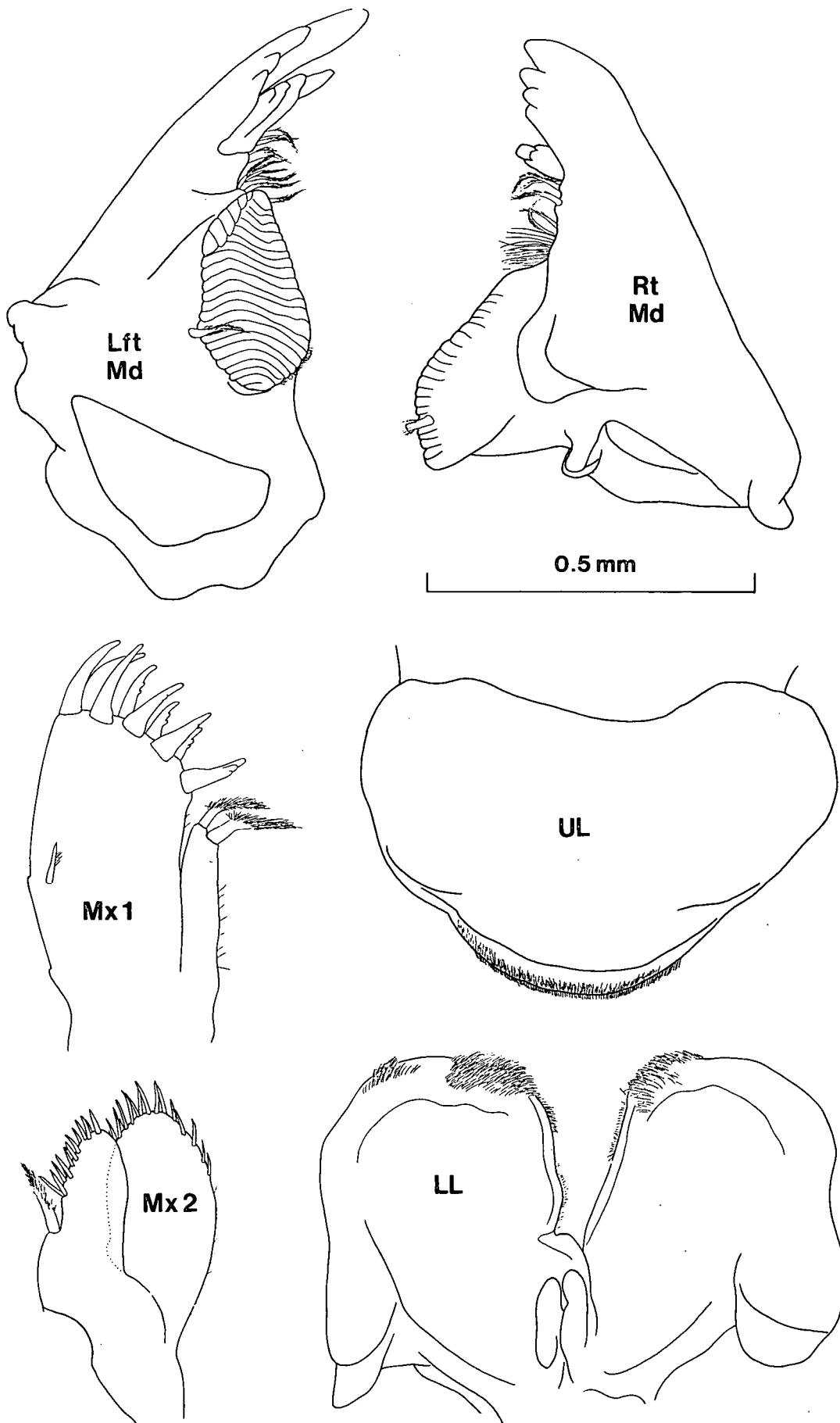


FIGURE 3.46 *Keratroides albus* gen. et sp.n., holotype ♀.

2 flagellum 15-segmented [7-15].

Gnathopod 2, hind lobes of segments 4 and 5 smaller, distal lobe of segment 6 broader than in ♀.

Otherwise similar to ♀, but bearing paired ventral penes and lacking oöstegites.

Remarks

This aberrant species is a specialised burrower found in western Tasmania. Specimens were found in distinct burrows in clay beside the Magnet Mine road, near Waratah, and at the type locality. In other areas, *K. albus* sp.n. was collected at depths to 20 cm in the soil, but burrows were not detected (although they may have been disturbed by digging).

Many of the unusual features displayed by this amphipod may be related to the burrowing habit, and several are also found in *K. angulosus* (q.v.). These features include:

short, strong peraeopods and (especially) gnathopod 1;

short antennae;

lack of body pigment (see Section 7.3);

small eyes (see Section 7.3);

rounded cephalon (see Section 7.3);

pleopods 1 and to a lesser extent 2 very broad, due to secondary broadening of peduncle, forming a movable septum across the ventral tunnel; (perhaps this is important in aeration in burrows);

mouthparts different from usual *Keratroides* morphology, indicating a different diet, perhaps plant roots; differences especially noticeable in mandibles, maxilla 2 and maxillipeds (palps very slender, outer plate pointed, not truncate, bearing only one group of apical spines);

peraeopod 6 gill proximally very large;

Body broad and shallow, almost dorsoventrally compressed, coxae very small; strength and a circular body section are apparently more

important than the ability to slip between leaves (to which the laterally flattened shape of other landhoppers has been attributed).

These animals move slowly when disturbed, not jumping effectively. Amphipods of an unrelated species from New Caledonia display the same general facies as *K. albus*, sp.n. indicating that this morphology has resulted from adaptation to a particular niche.

Adult *K. albus*, sp.n. are fairly large animals (some over 15 mm long), and there is no size difference between the sexes. Large size may be an advantage to a burrowing amphipod, perhaps bestowing more strength, and this would apply equally to both sexes; in other species females are large, allowing more eggs to be brooded, but males are smaller, apparently at an ideal size for a non-brooding existence.

This species is difficult to place in the generic structure used in this work and there is some justification for erecting another genus to receive it. This is because the radical morphological changes caused by adaptation to the burrowing habit have affected several of the features used for generic definition.

The maxilliped outer plate, mandible, maxilla 2, gnathopod 1, pleopods and elongate terminal spines of the dactyls are unlike those of any other species in either *Keratroides* or *Arcitalitrus*, although this species is otherwise close to both genera. The species is here placed in *Keratroides* because of the following features:

- 1) its lack of oöstegites on the ♀ second gnathopods;
- 2) the presence of a long spine proximally on the anterior margin of segment 2, gnathopod 2;
- 3) the concave distal margin of epimeral plate 3.

Keratroides vulgaris (Friend)

Figures 3.47 - 3.49

Talitrus sylvaticus. Thomson, 1893 (*partim*)

p.59, pl.iv, figures 1, 3, 4, 7, 9, 10

Talitrus (Talitroides) sylvaticus. Ruffo, 1949 (*partim*) p.206*Talitrus kershawi*. Hurley, 1955, p.155, figure 4.*Talitrus (Keratroides) vulgaris* Friend, 1979, p.85, figures 1a, 2, 3.

Types:

Holotype ♀ (ovig., 3 eggs), TMAG (Tasmanian Museum and Art Gallery), G1945; Gully near Strickland Ave., foothills of Mt. Wellington, near Hobart, Tasmania, under leaf litter, *Atherospermum moschatum* stand. UGR 8312-213485. Coll. JAF, 20.xi.1977. Allotype ♂, TMAG, G1946; same data as holotype. Paratypes 11 ♂♂, 9 ♀♀ (1 ovig.), 5 imm. TMAG, G1947; same data as holotype; ♂, TMAG, G1948; same data as holotype; 1 imm., TMAG, G1949; Under leaf litter, *Olearia argophylla* stand near Anglers Ck., off Tower Rd., Tooms Lake area, E. Tasmania. UGR 8413-702229. Coll. JAF, 12.i.1976.

Other material examined: TASMANIA:

1 specimen, Museo Civico di Storia Naturale, Genova; Mt. Wellington, coll. E. d'Albertis and O. Beccari, 12.ii.1878. 4 ♀♀ (4 ovig.) Australian Museum, G5422; "Tasmania, old colln.". 2 specimens, South Australian Museum, TC902; Lady Barron Falls, National Park, pres. G.P. Whitley, 19.i.1928. 2 ♂♂, 7 ♀♀, National Museum of Victoria; Kingston, coll. C. Oke, 14.v.1948.

7815-1(4), -2(17), -3(13), -4(8), -5(7), -6(33), -7(13), -8(8),
-9(2), -10(54), -11(20), -12(30), -13(8), -14(5), -15(1), -16(2),
-17(6), -18(4), -19(1)

7816-7(7), -9(22), -12(15), -15(1), -16(20), -17(45), -18(20),
-19(4), -21(27), -22(3), -23(28), -24(1)

7913-1(6), -2(21), -3(1), -4(17), -8(29), -9(2), -11(60), -12(9)

7914-1(12), -2(4), -3(2), -4(9), -5(2), -8(5), -9(4)

7915-1(14), -3(23), -4(2), -5(2), -6(5), -9(18), -10(13), -11(19),
-12(4), -13(2), -14(6), -15(3), -17(11), -18(17), -19(4), -20(8),
-21(19), -22(12), -23(20)

7916-1(1), -2(6)

8012-3(3), -4(18), -5(6), -6(2), -7(1), -8(15), -9(4), -10(7), -11(5)
-12(1), -13(6), -14(1), -15(1), -21(3), -23(8), -24(10), -27(3),
-28(3), -29(3), -30(18), -31(7), -32(6), -33(11), -34(7), -35(1),
-36(12), -37(17), -38(47), -39(153), -40(21), -41(3), -42(5), -43(2),
-44(4), -45(21), -47(18), -48(5), -49(3), -50(7), -51(21), -52(4),
-53(45), -55(14), -56(21), -57(17), -58(6), -59(3), -60(4), -62(2),
-63(10), -65(8), -66(4), -67(15)

8013-1(31), -2(39), -3(111), -4(5), -5(1), -6(25), -7(2), -8(18),
-9(29), -11(56), -12(54), -13(6), -14(8), -15(2), -16(3), -17(1),
-18(16), -19(2), -22(13), -23(3), -24(2), -25(1), -30(39), -31(429),
-32(89), -33(21), -34(6), -35(20), -37(35), -38(16), -39(14), -40(2),
-41(26), -42(22), -43(217)

8014-1(1), -3(7), -4(3), -5(5), -6(1), -7(6), -8(1), -9(1), -10(2),
-11(10), -12(8), -15(1), -16(3), -17(1), -18(14)

8015-1(40), -2(2), -3(15), -4(40), -5(21), -6(24), -7(2), -9(40),
-10(9), -11(17), -12(2), -13(41), -14(18), -15(11), -16(23), -17(29),
-18(14), -19(16), -21(10), -22(1)

8016-1(22)

8110-11(14), -12(11), -14(6), -15(5), -16(2), -23(54), -24(5)

8112-1(13), -2(22), -3(6), -4(20), -5(15), -6(4), -7(11), -8(9),
-9(5), -10(7), -12(2), -14(45), -15(25), -16(10), -17(11), -18(3),
-19(3)

8113-1(4), -2(27), -3(9), -4(8), -5(26), -6(3), -7(3), -8(6), -9(22),
-11(9), -12(33), -13(11), -14(1), -15(23)

8115-1(9), -2(34), -3(3)

8210-3(4), -5(4), -6(30), -10(1), -13(2), -18(2), -20(43), -21(10),

-22(15), -23(2)

8211-1(4), -4(3), -5(61), -6(9), -7(10), -8(4), -9(1), -10(25),
-11(5), -12(1), -14(2), -16(9), -18(4), -22(4), -30(40), -31(1)

8212-1(12), -2(2), -3(5), -4(20), -5(6), -6(2), -7(7), -8(1),
-9(1), -11(2)

8213-1(47), -2(13)

8214-1(28), -2(7), -3(21), -4(13), -5(33)

8215-1(1), -2(106), -3(4), -4(117), -5(327), -6(181)

8311-2(1), -6(6), -7(2)

8312-1(2), -2(1), -3(3), -4(5), -7(45), 15(1)

8313-1(21), -2(24)

8315-1(39), -2(5), -3(7)

8411-2(6), -3(33), -4(14), -6(10), -7(21)

8412-3(6), -8(22), -9(1), -10(14), -11(1), -13(3), -17(8)

8413-1(14), -2(6), -3(42), -4(3), -5(26), -6(32), -7(20), -8(1),
-11(1), -13(15), -14(6), -15(5), -16(21), -17(20), -18(12), -19(2),
-20(6), -21(7), -22(37), -23(50), -24(1), -25(1)

8414-1(1)

8415-2(1), -3(9), -4(23), -5(26), -6(8), -7(34), -8(4), -9(40),
-10(88), -11(57), -12(81), -13(260), -14(50), -15(92), -16(94),
-17(29), -18(2), -19(174)

8416-2(21)

8512-1(25), -2(3), -4(11), -6(6)

8513-3(4), -4(20), -6(3)

8514-1(11), -2(21), -3(35), -4(10), -5(14), -6(9), -7(2), -10(11)

8515-2(32), -3(24), -4(8), -5(17), -6(1), -7(6), -8(5), -9(1), -10(14)

8516-2(28)

Diagnosis

A large landhopper of the genus *Keratroides* with dorsal surface of head gently rounded, second antennae longer than head and first four

peraeon segments, oostegites with long apical setae, third epimeral plate deeper than second, front corner rounded, lower margin concave; pleopods reduced to stumps with or without vestigial rami; posterior gill anseriform, with a slender linear or curved distal extension.

Description

Female:

Length 11.5 mm. Head as long as deep, dorsal surface gently curving. Eye round, about one third as wide as head is long. Antenna 1 short, almost reaching middle of distal peduncular segment of antenna 2, flagellum of five segments [3-5], shorter than peduncle. Antenna 2, flagellum of 24 segments [8-28], each bearing four groups of three spines, except the distal segment, which bears a group of six or more, and the proximal segment, single spines; peduncle shorter, distal segment as long as penultimate two combined.

Upper lip shallow, broad, apically pilose, indentation on right margin present. Lower lip broad, inner shoulders pilose, sides of central trough lightly pilose. Mandible, incisor 3-toothed, left lacinia mobilis bicusate, large cusps with four teeth, molar process well developed. Maxilla 1, inner plate short, narrowing distally, inner margin setose, outer plate setulose proximally, palp situated distal of midpoint of outer margin, very small, two-jointed.

Maxilla 2, outer plate the longer, outer margin bearing five small teeth distally.

Maxilliped, inner plate with setose spines distally, three terminal teeth, inner small, others larger; outer plate short, narrowing distally, apex truncate and bearing spine groups at the corners (two spines on outer, nine on inner corner). Palp slender, bearing a few long spines, fourth segment delimited proximally by a slight shoulder.

Gnathopod 1, coxal plate broad with obtusely rounded distal margin

supplied with small spines. Segment 2 broadening slightly distally, poorly spined. Segment 3 shorter than 4, which bears a shallow posterior lobe. Segments 5 and 6 short, equal in length, segment 5 expanded deeply into a scabrous posterior lobe. Segment 6 gently narrowing distally, with strongly spined posterior margin forming a simple hand with the strong dactyl.

Gnathopod 2, coxal plate subsquare, gently rounded below, posterior process very small, obtusely rounded. Gill large, with anterior and wide posterior extensions. Oöstegite entirely absent. Segment 2 linear, with several large anterior spines. Segment 4 subequal to segment 3, with large scabrous tumid posterior lobe. Segment 6 equal in length to segment 5, both with scabrous posterior surfaces. Dactyl strongly exceeded by sharp apical lobe.

Peraeopods long, slender, larger spines bifid, especially on distal segments. Peraeopods 3 and 4, coxal plate deep, subquadrate, posterior process small, sharply rounded. Gill small, wider posteriorly. Oöstegite narrow, linear, with six long apical setae.

Peraeopod 5, anterior coxal lobe shallow, lower margin oblique, lightly spinulose; posterior lobe smaller, shallow, sharply rounding to slightly excavate posterior margin. Gill small, convoluted, reduced oöstegite of gill-like texture, held laterally across ventral surface. Dactyl slender, terminal spine curved.

Peraeopod 6, posterior coxal lobe moderately deep, squarish distally, hind margin smoothly rounded, weakly serrate; anterior coxal lobe rounded distally, front margin gently excavate. Gill long, anseriform, proximally convoluted, then flattened, narrowing distally, with a slender linear distal extension. Segment 2 subovate, posterior margin spinulose, distal lobe very small. Segments 4-6 slender, spinose. Dactyl slender, terminal spine long.

Peraeopod 7, coxal plate subrectangular, posterodistally rounded and minutely serrate, with proximal anterior process. Segment 2 sub-

circular, posterior margin weakly serrate, distal lobe shallow.

Segments 4-6 slender and spinose, dactyl slender, terminal spine long.

Epimeral plate 1 shallow, distal margin very slightly oblique.

Posterior margin gently convex, weakly serrate and spinulose. Epimeral plate 2 subsquare, lower margin very gently rounded. Anterior corner round, anterior margin bearing one small spine. Posterior margin gently sinuous, weakly serrate and spinulose. Epimeral plate 3 exceeding second plate, lower margin gently convex, oblique anterior corner smoothly rounded; posterior margin gently sinuous, weakly serrate and spinulose along its length, posterior corner sharp.

Pleopods vestigial; peduncle of first short and slender, outer margin gently concave, inner bearing two coupling spines; a short terminal one-segmented ramus present [sometimes two rami]: pleopod 2 similar, but both peduncle and ramus shorter; pleopod 3 reduced to a minute stump, with [or without] a small spine. [First instar specimens; pleopods reduced, peduncle of first short, slender, outer margin gently concave, bearing two coupling spines and sometimes a short simple spine; two unequal one-segmented rami present, the outer the longer, each with two long (and sometimes a shorter third) plumose setae, with thicker proximal and thinner distal portions. Second pleopod like that of adult, or with peduncle very short, outer margin slightly concave, bearing two coupling spines; a one-segmented ramus present, with one long apical plumose seta. Third pleopod a minute stump as in adult specimens.]

Uropod 1, peduncle long, slender, with two subterminal spines, interramal spine long, simple. Rami slender, shorter than peduncle, inner with two marginal spines, outer smooth. Uropod 2, peduncle as long as rami, with two spines near distal end; inner ramus with one marginal spine, outer ramus smooth. Uropod 3 very small, peduncle short, bearing one large lateral spine and several spinules, ramus small, conical with one small and one minute apical spine. Telson longer than wide, widening distally, apex rounded, slightly emarginate, one apical and five [up to

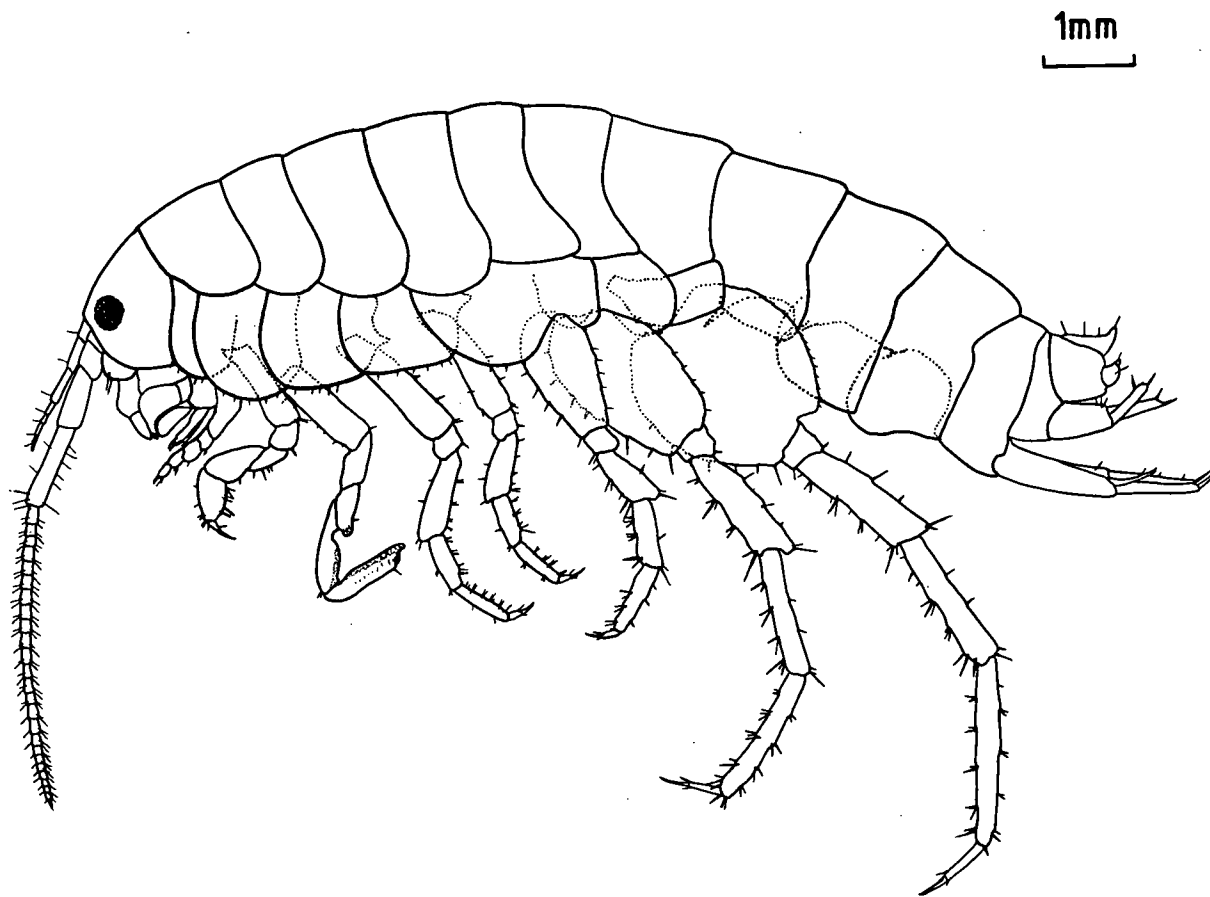


Figure 4.47 *Keratroides vulgaris* (Friend) gen.n., holotype ♀.

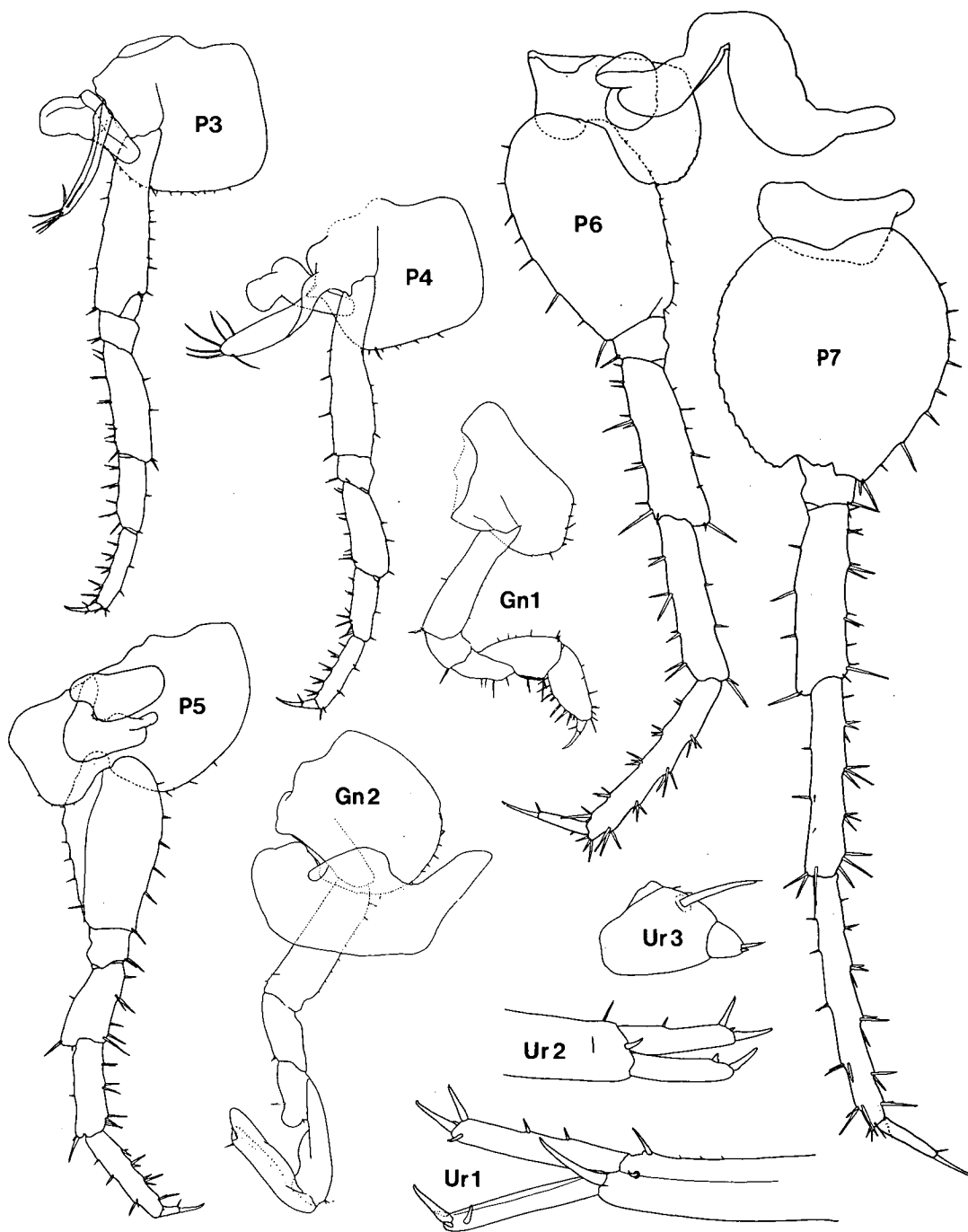


Figure 3.48 *Keratroides vulgaris* (Friend) gen.n., holotype ♀.
 Ur1-3: uropod 1-3. Gn1&2, P3-7: x20. Ur1&2: x30.
 Ur3: x60.

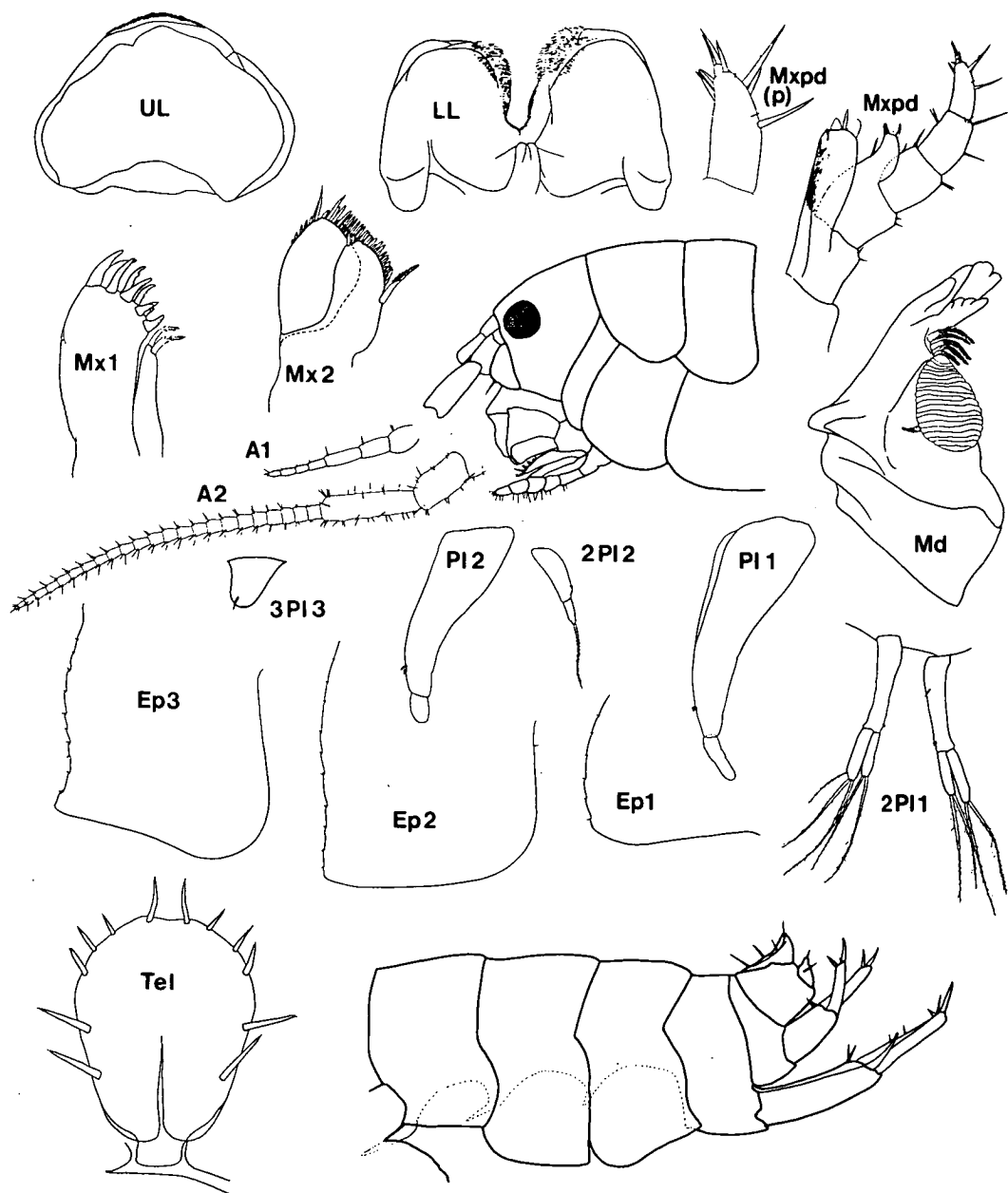


Figure 3.49 *Keratroides vulgaris* (Friend) gen.n., holotype ♀. 2, first instar juvenile, 4 mm, Anglers Ck. 3, ♂, 10.4 mm, type locality. A1&2: antenna 1 & 2. Md: left mandible. Mxpd (p): distal segments of maxilliped palp. Head, abdomen, A1&2: x15. UL, LL, Md, Mx1&2: x50. Mxpd: x40. Mxpd(p): x85. PI1&2, 2PI1&2: x75. PI3: x100. Ep1-3: x30. Tel: x50.

five, usually four] marginal spines on each side.

Male:

Length 10.8 mm. Like ♀, but bearing paired ventral penes on peraeonite 7 and lacking oöstegites.

Remarks

The most common species in Tasmania, *K. vulgaris* is distinguished from other *Keratroides* species by its long second antennae, its distinctive gill shape and the shape and size of its epimeral plates.

Individuals of both sexes grow to a large size (15 mm), and breeding apparently occurs only during the warmer months (Chapter 8) when broods of up to 12 eggs are produced. This is an active species living in the upper litter/soil layers, as demonstrated in Chapter 7; when disturbed, *K. vulgaris* hop and flip vigorously to a place of shelter.

As used here, *K. vulgaris* includes several forms which may prove to be distinct, and to warrant specific recognition. For instance, a proportion of specimens from north west Tasmania have two equal slender rami on pleopod 1, while others in the same sample have only one relatively long ramus on pleopod 1, and some have a long curved distal lobe on the gill of peraeopod 6.

The synonymies listed above have been explained previously (Friend, 1979).

Keratroides rex, sp.n.

Figures 3.50 - 3.54

Types:

Holotype ♀; Currie, King I., 200 m from sea, in scrub under two eucalypts. UGR 7719-299748. Coll. GE, 19.iv.1976 (7719-2).

Allotype ♂; same data as holotype. Paratypes, 3 ♂♂, 19 ♀♀ (11 ovig.), 8 imm.; same data as holotype.

Other material examined: TASMANIA:

7816-2(47), -3(42), -4(51), -5(22), -7(23), -9(7), -10(2),
-12(18), -13(7), -14(23), -16(2), -20(19)

7817-1(2)

7913-6(1), -7(8), -8(5)

8011-3(2), -5(many)

8110-1(14), -2(66), -3(23), -9(47), -10(47), -16(40), -22(48)

8115-3(15)

8215-7(57)

Diagnosis

A medium-sized landhopper of the genus *Keratroides* with fairly short antennae, very short non-setose oöstegites on peraeopods 3 and 4, vestigial pleopods, epimeral plate 2 the longest, plate 3 round in front and straight below, with two long proximal spines on each side of the telson.

Description

Female:

Length 8.3 mm with no eggs [1+]. Head longer than broad, dorsal surface gently curving. Eye medium, round, width less than one-third head length. Antenna 1 short, just exceeding distal end of fourth peduncular segment of antenna 2; flagellum shorter than peduncle, consisting of five segments [3-5]. Antenna 2 longer than head and first three

peraeon segments, peduncular segment 5 just shorter than rest of peduncle; flagellum longer than peduncle, comprising 20 short segments [8-20], each bearing four groups of 2-3 bristles.

Upper lip broad, apex lightly pilose, indentation of right margin marked. Lower lip broad, lateral lobes shallow, inner shoulders moderately pilose, margins of central cleft almost naked. Left mandible, incisor 5-cusped, lacinia mobilis 4-toothed, molar process strong, triturating surface bearing 15 ridges, upper edge raised in a low rim; right mandible, incisor 5-toothed, lacinia 3-cusped, with distal field covered in tiny bumps. Maxilla 1 broad, inner plate short, wide, terminal plumes slender; outer plate broad distally, 2-segmented palp near midpoint of outer margin, apical spines strong, toothed, innermost leaning inwards, almost lateral; dentition formula 0-0-0-4-3-4-2-4-2. Maxilla 2 broad, inner plate almost as broad and as long as outer plate, bearing well-separated blunt spines, all short except innermost two, plumose seta long, inner margin of plate setose; outer plate apex broadly rounded, outermost spines long and sharp, remainder of spine-row composed of fairly long blunt spines and short, oblique-tipped ones.

Maxilliped, inner plate fairly broad, apex truncate, outer spine-tooth large, and rounded, middle spine-tooth smaller, inner one tiny, apex also bearing a long blunt spine; no plumose spines on lateral face, medial face with two inner marginal plumes and one subapically. Outer plate apex truncate, with two stout sharp spines on the outer corner, a group of six slender spines at the inner corner, which is extended in a rounded projection; inner margin with a group of two spines, and two single proximal spines. Palp slender, segments 2 and 3 with narrow remnants of lateral lobes, with a small group of spines distally on each lobe; segment 4 prominent, distinct, unmasked by segment 3, conical with an apical group of three spines.

Gnathopod 1 coxal plate broad, distally truncate, inner shelf absent. Segment 2 fairly short, bearing spines on both margins. Segment 4 with a very small scabrous blister, moderately spinose behind. Segment 5 short, deep, bearing several spines and a prominent broad posterior tumescence. Segment 6 shorter than 5, gently narrowing distally, palm absent, posterior margin equipped with numerous strong spines, powerful dactyl with a strong curved terminal spine.

Gnathopod 2, coxal plate deeper than broad, lower margin rounded, spinulose; posterior process small, obtuse. Gill large, proximal lobe broad, anterior extension short, relatively broad; oöstegite completely absent. Segment 2, anterior margin expanded, bearing an even row of strong spines. Segment 4 with a weak posterior blister. Segment 5 elongate, bearing a few spinules only, posterior scabrous lobe long, deep, deeper distally. Segment 6 also elongate, just shorter, medial spine-row consisting of spinules, apical lobe subacute, strongly exceeding small dactyl.

Peraeopod 3, coxal plate as deep as broad, spinulose below, posterior process small, subacute. Gill club-shaped, slender distally, proximally lobate and held laterally across ventral surface; oöstegite rudimentary, short and slender, bearing no apical setae. Segment 2 strong, broadening distally. Segments 4-6 strongly spinose behind. Dactyl small, terminal spine short.

Peraeopod 4 shorter than 3, coxal plate broader than long, gently concave, spinulose below; posterior process long, slender, apically rounded, hooked downwards. Gill and oöstegite like those of peraeopod 3. Segments 2-6 similar but shorter than in 3, dactyl small, terminal spine short.

Peraeopod 5, anterior coxal lobe deep, posterior lobe shallower, distally truncate. Gill small, bilobate, oöstegite basally broad, narrowing to an acutely rounded apex, texture gill-like. Segment 2 long-ovate, posteriorly indented, spinose. Segments 4-6 strong, spinose in

front, dactyl slender, terminal spine short, curved.

Peraeopod 6, anterior coxal lobe shallow, anterior margin of hind lobe oblique, distally strongly rounded, expanded behind. Gill large, anseriform, subdistally broad, with a small, broad distal posterior lobe. Segment 2, long-ovate, serrulate behind, flat distal lobe present. Segments 4-6 strong, very spinose. Dactyl elongate, terminal spine slender.

Peraeopod 7, coxal plate broad, shallow. Segment 2 large, longer than broad, expanded behind, distal lobe shallow. Segments 4-6 strong, spinose. Dactyl slender, elongate, terminal spine slender.

First epimeral plate shallow, lower margin slightly oblique, hind corner rounded, posterior margin convex. Second plate the deepest, front corner gently rounded, lower margin oblique, higher in front, hind corner rounded, hind margin weakly crenate, almost straight. Third plate subsquare, front corner strongly rounded, lower margin slightly concave, hind corner fairly sharp, posterior margin convex, serrulate and spinulose.

Pleopods vestigial, second and third very small. First pleopod uniramous, peduncle narrowing distally, curving outwards, no coupling spines present, distally produced into a rounded projection beside the single (outer) ramus, which is one segmented and papillate. Second pleopod a stump, one-third as long as first pleopod, bearing a single subapical spinule. Third pleopod one-quarter as long as second, as broad as long, with two marginal spinules.

Uropod 1, peduncle strong, with two outer and one inner marginal spine, apical spine slender, slightly curved; rami subequal, shorter than peduncle, outer the more slender, margins bare; inner ramus bearing two marginal spines. Uropod 2, peduncle bearing one inner marginal spine, outer margin with a short proximal spine and two distal spines close together; outer ramus slightly the longer, margins naked, inner ramus with one proximal marginal spine. Uropod 3 small, peduncle short

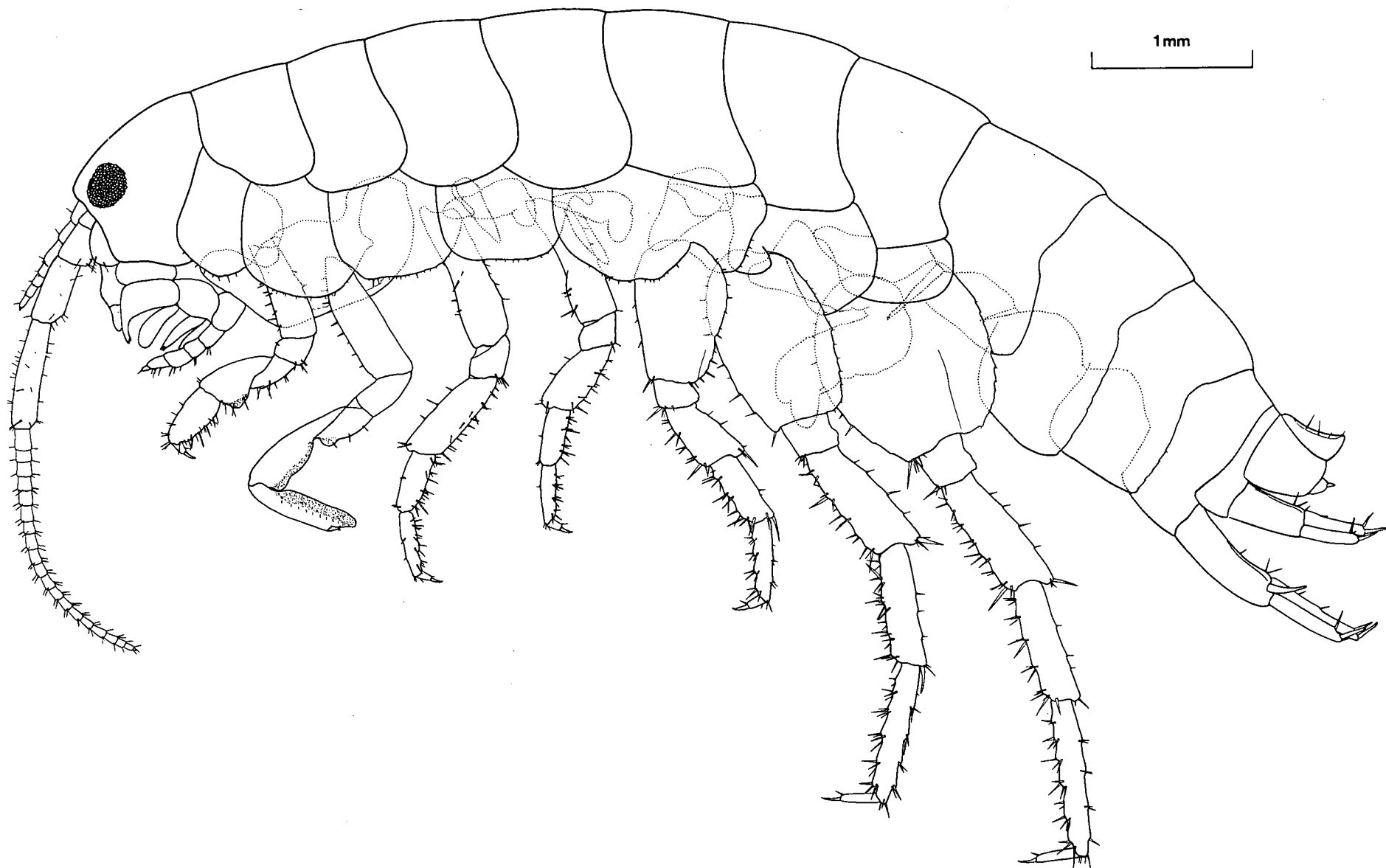


FIGURE 3.50 *Keratroides rex* gen. et sp.n., holotype ♀.

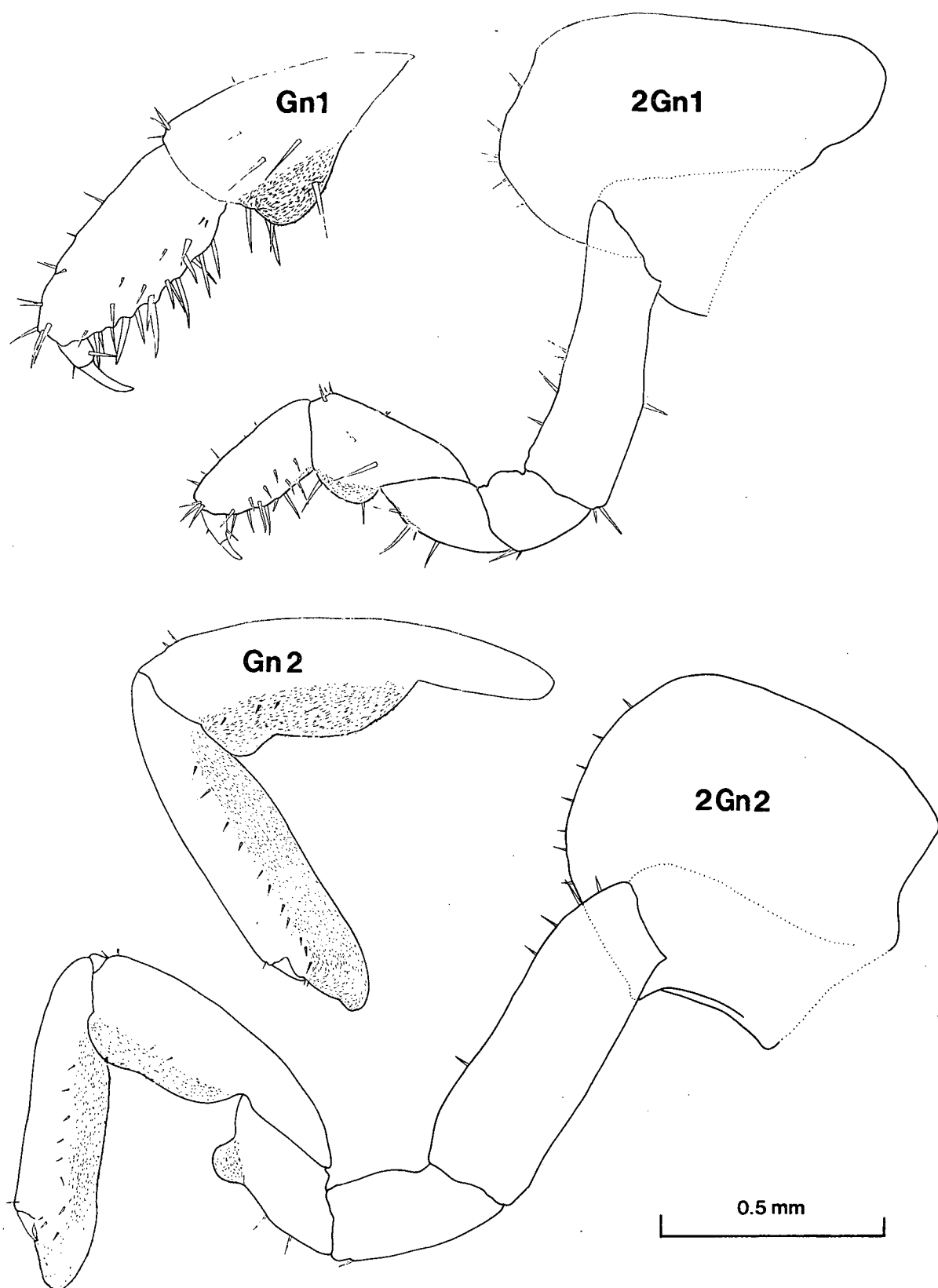


FIGURE 3.51 *Keratroides rex* gen. et sp.n., holotype ♀. 2, allotype ♂.

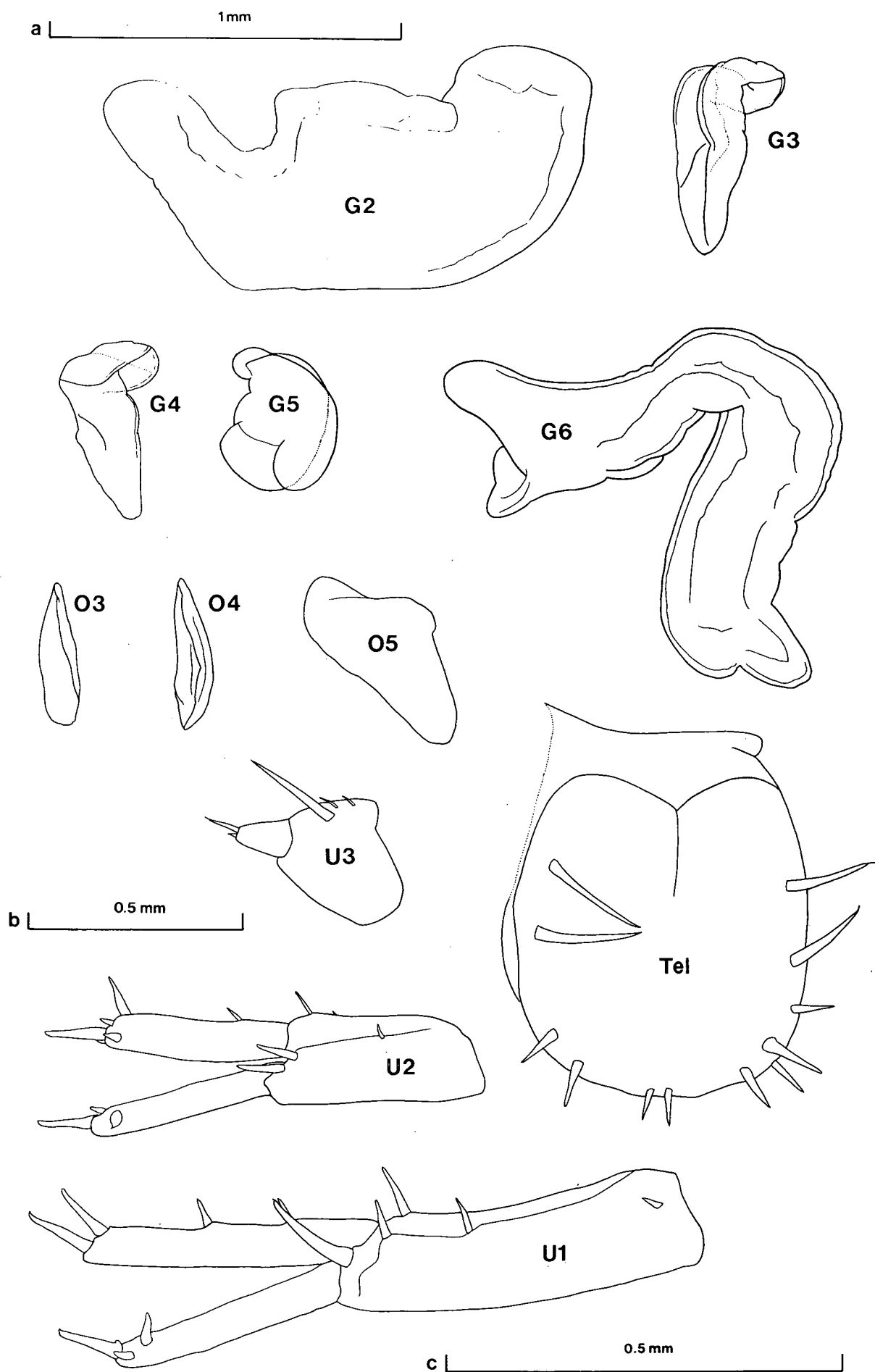


FIGURE 3.52 *Keratroides rex* gen. et sp.n., holotype ♀. Scale a; G2-6, O3-5, U1&2. Scale b; Tel, U3.

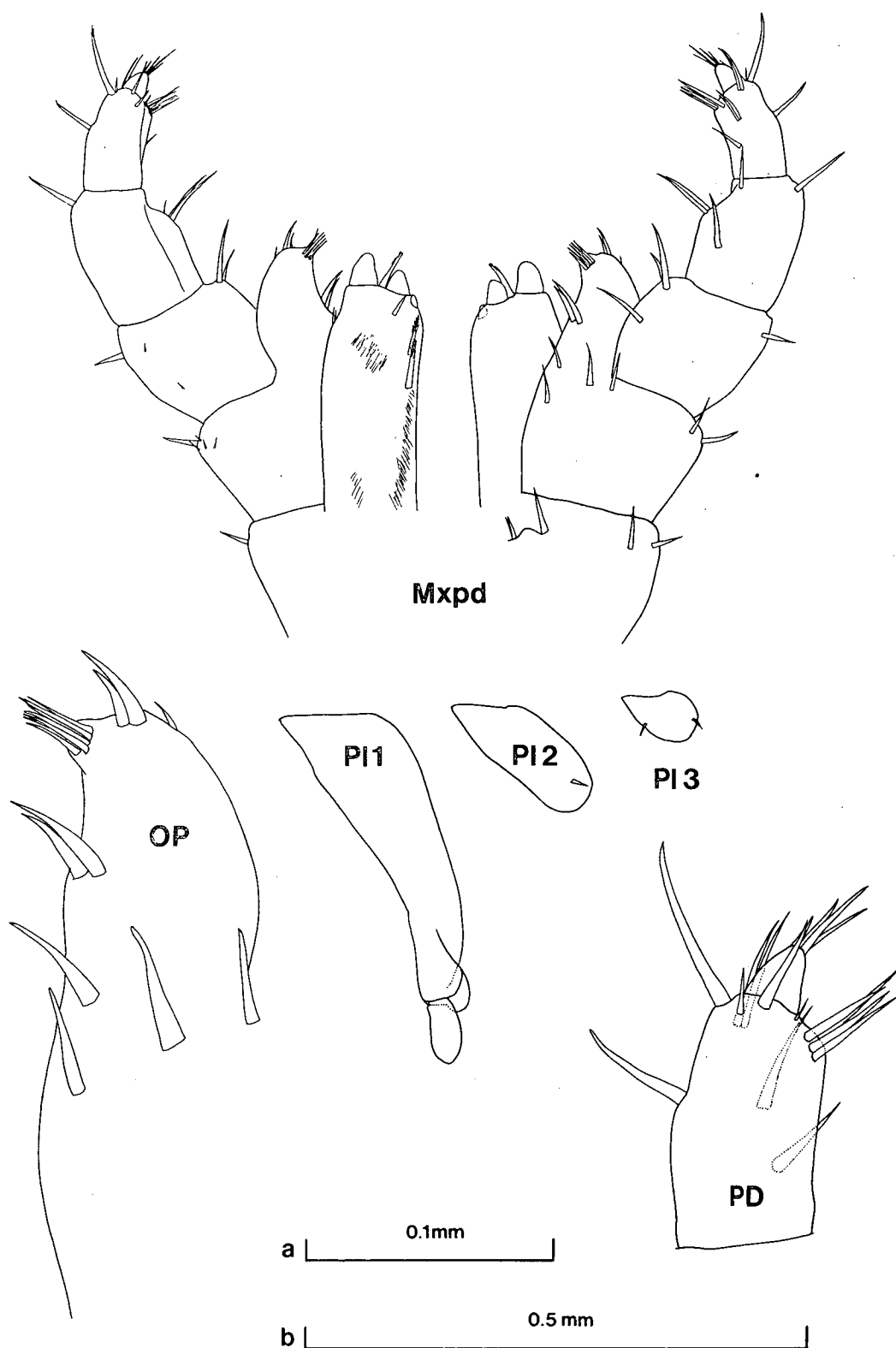


FIGURE 3.53 *Keratroides rex* gen. et sp.n., holotype ♀. Scale a; OP, PD. Scale b; Mxp, PI1-3.

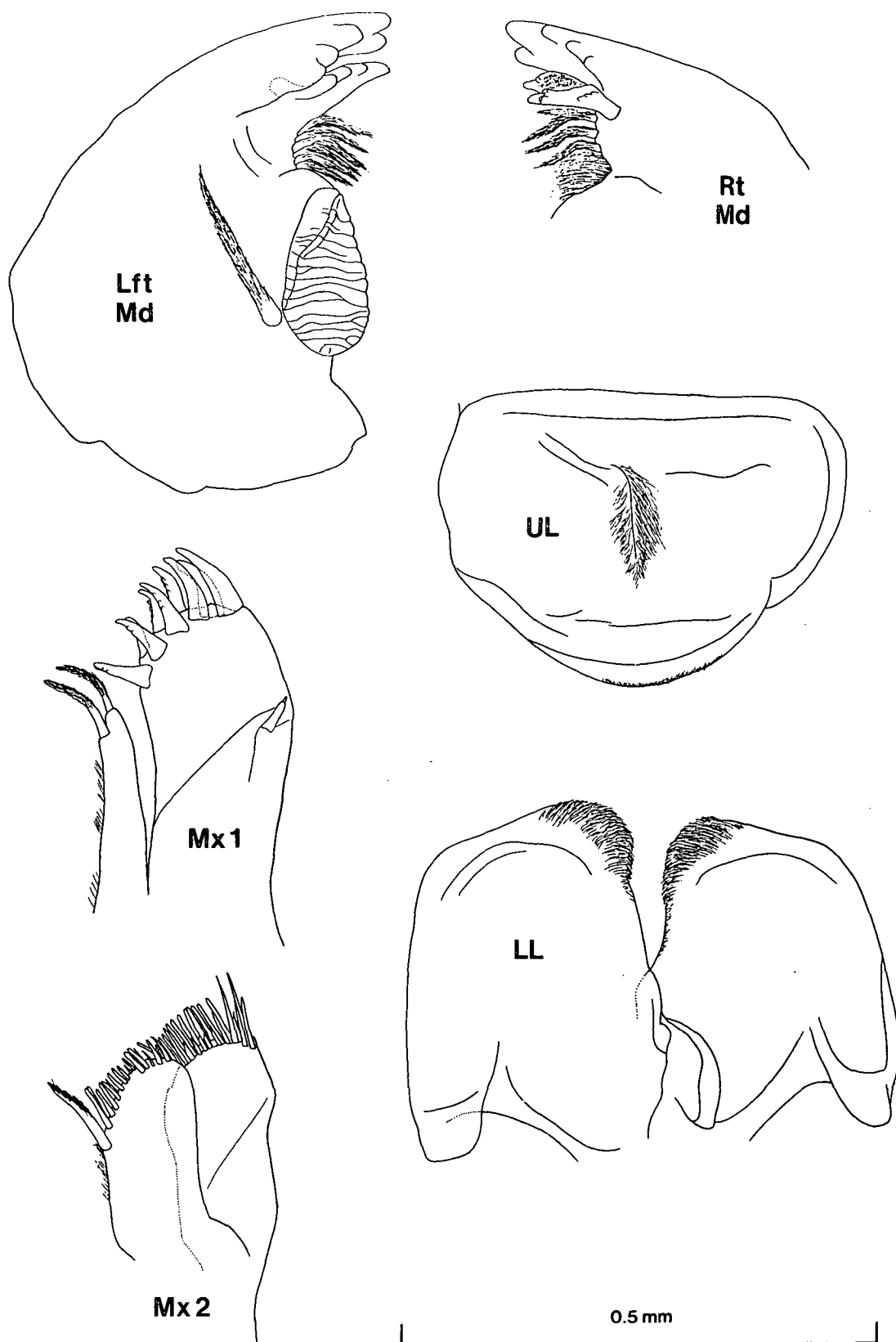


FIGURE 3.54 *Keratroides rex* gen. et sp.n., holotype ♀.

and broad with one large spine and two spinules close together; peduncle short bearing two unequal spines at the apex.

Telson broad, apex broadly rounded, almost truncate, entire each side, bearing one small apical spine and 4-6 marginal spines, including two long bifid spines mid-marginally.

Male:

Length 5.5 mm. Antenna 1, flagellum comprising 4 segments [3-5]. Flagellum of antenna 2, 18-segmented [8-19].

Otherwise like ♀ but lacking oöstegites and bearing paired ventral penes on peraeonite 7.

Remarks

Keratroides rex sp.n. is close to *K. vulgaris* but is distinguished from it by the possession of second epimeral plates which are longer than the third pair, and distally broad peraeopod 6 gills indented apically, forming a short posterior lobe. It is found only near the coast on the mainland of Tasmania, and on offshore islands, occurring as far north as King Island (to which the name refers).

Females of *K. rex* sp.n. are larger than males; their oöstegites are short and lack setae, allowing eggs to fall out easily during preservation.

Keratroides pyrensis, sp.n.

Figures 3.55 - 3.59

Types:

Holotype ♀ (ovig., 1 egg); The Bottleneck, Ansons R., right bank of small tributary on S side, in damp mud under stones on banks. UGR 8515-035538. Coll. AMMR, 8.xi.1977 (8515-6). Allotype ♂; same data as holotype. Paratypes 6 ♂♂, 2 ♀♀ (1 ovig.), 4 imm; same data as holotype.

Other material examined: TASMANIA:

8315-4(43)

8415-4(23), -17(26)

8515-1(25), -2(32), -5(10), -8(2), -9(18), -10(5)

Diagnosis

A medium-sized landhopper similar to *K. vulgaris*, but with distal segments of ♂ gnathopod 1 heavier than in ♀, distal lobe of gnathopod 2 acutely rounded, gill of peraeopod 6 evenly tapering distally, margins crenulate, pleopods 1 and 2 with apical plumose setae on the ramal vestiges and second epimeral plate deeper than third.

Description

Female:

Length 9.0 mm, ovigerous, bearing 1 egg [2]. Head deeper than long, dorsal surface gently curving, eye large, width about two-fifths head length. Antenna 1 reaching about one-third distance along last peduncular segment of antenna 2; flagellum shorter than peduncle, six-segmented [3-6]. Antenna 2 long, longer than head and first five peraeon segments, last peduncular segment as long as rest of peduncle; flagellum longer than peduncle, comprising 26 slender segments [8-28], most of which bear four groups of 3 long bristles.

Upper lip broad, apically pilose, indentation of right margin prominent. Lower lip broad, lateral lobes fairly small, inner shoulders with long pilosity, margins of central cleft very lightly pilose. Left mandible, incisor 5-cusate, lacinia mobilis 4-cusate, molar process strong, triturating surface with 15 striae; right mandible, incisor 5-toothed, lacinia 3-cusate, with a distal field of tiny bumps, proximal ridge bearing a number of larger rounded denticles. Maxilla 1, inner plate short, terminal setae small; outer plate broadening distally, palp small, slender, 2nd segment minute, distal spines large, innermost leaning inwards, almost laterally oriented, dentition formula 0-0-0-3-2-3-2-2-2. Maxilla 2, broad, inner plate much narrower than outer, plumose seta long, apical spines longer towards inner margin; outer plate apex broadly rounded, two long spines near apex, other spines well-separated, blunt-ended.

Maxilliped, inner plate quite broad, apex truncate, bearing two large and one small spine-tooth and a longer stout blunt spine; two short spines on outer margin, medial face bearing a small subapical plumose seta and two larger ones on the inner margin, lateral surface with two plumose setae subapically. Outer plate apex truncate, with a spine-group at each corner, two on the outer and five on the inner corner; inner margin with a pair of spines more proximally. Palp slender, bearing a few long, slender spines, second and third segments with vestigial lateral lobes, each bearing two long slender spines on the inner margin; fourth segment laterally fused with third, basally broad, conical, with two apical spines.

Gnathopod 1, coxal plate deep, broad, lower margin sparingly spinose, inner shelf vestigial. Segment 2 slender, curving anteriorly, with a large spine near middle of hind margin. Segment 4 with a small posterior blister, spinose behind. Segment 5 short, deep, moderately spinose, hind lobe substantial, rounded. Segment 6 short, not as long as 5, proximally broad but narrowing distally to base of dactyl, no palm

present, spinose posteriorly with several stout spines. Dactyl very strong, half as long as segment 6, terminal spine long and curving.

Gnathopod 2, coxal plate deep, posterior process prominent, acute. Gill large, anterior extension long, broad, apically rounded, oöstegite absent. Segment 2 slightly expanded and spinulose in front, bearing one large spine proximally on front margin. Segment 3 longer than 4 which is poorly spinose and bears a small prominent scabrous lobe behind. Segment 5 elongate, posterior lobe shallow, over half as long as segment, almost free of spines. Segment 6 as long as 5, slender, distal lobe long, acutely rounded, medial spine-row composed of ten evenly-spaced, small spines. Dactyl small.

Peraeopod 3, coxal plate large, subsquare, posterior process subacute, lower margin spinulose. Gill club-shaped, slender proximally, distally lobate, held across ventral surface; oöstegite narrow, bearing four slender apical setae. Segment 2 long, heavy, one large spine on posterior margin. Segments 4-6 slender, moderately spinose. Dactyl slender.

Peraeopod 4, coxal plate broader than deep, lower margin straight, posterior process sharp, hooked. Gill like that of peraeopod 3, oöstegite with seven apical setae. Segments 2-6 shorter than in 3.

Peraeopod 5, coxal lobes of similar depth, posterior lobe slightly concave behind. Gill very small, bilobed; oöstegite broad proximally, short, apically bearing a tuft of long hairs. Segment 2 narrowing distally, serrate but almost straight behind. Dactyl slender, quite long.

Peraeopod 6, anterior coxal lobe shallow, posterior lobe smoothly rounded. Gill anseriform, tapering smoothly towards apex, margins distally crenulate. Segment 2 large, slender-ovate, hind margin meeting trunk of segment subdistally. Segments 4-6 long, slender, spines quite long, dactyl very long, slender, terminal spine almost straight.

Peraeopod 7, coxal plate very shallow, spinulose posterodistally.

Segment 2 large, broadly ovate, distal lobe shallow. Segments 4-6 slender, spinose, dactyl very long.

First epimeral plate shallow, lower margin slightly oblique, concave and serrulate behind. Second plate the longest, smoothly rounded in front and below, hind corner obtuse, minutely produced; posterior margin almost straight, serrulate. Third plate subsquare, anterior corner rounded, lower margin oblique, gently convex, hind corner quite sharp, margin gently sinuous, serrulate.

Pleopods all vestigial, progressively smaller posteriorly. First pleopod, peduncle narrowing distally, bearing two coupling spines; biramous, both rami single segmented, outer longer and bearing two apical plumose setae, inner with an apical seta. Second similar, but with only one ramus, which bears one apical seta. Third pleopod a minute peduncular vestige bearing two small spines.

Uropod 1 long, peduncle slender, inner margin lined with tiny spinules, one distal spine on each margin, apical spine long, slender and curved; rami subequal, shorter than peduncle, margins of outer ramus smooth, inner bearing three marginal spines. Uropod 2 peduncle longer than rami, with a spine distally on each margin; outer ramus marginally naked, inner with two spines near proximal end. Uropod 3 short, peduncle broad, bearing one large lateral spine and three spinules; ramus short, conical, two small unequal spines apically.

Telson large, quite broad, apex broadly re-entrant, three marginal and one apical spine on each side.

Male:

Length 7.7 mm. Antenna 1, flagellum comprising 6 segments [3-6]. Antenna 2 flagellum 27-segmented [8-27].

Gnathopod 1, segments 5 and 6 heavier than those of ♀.

Otherwise like ♀ but lacking oöstegites and bearing paired penes ventrally.

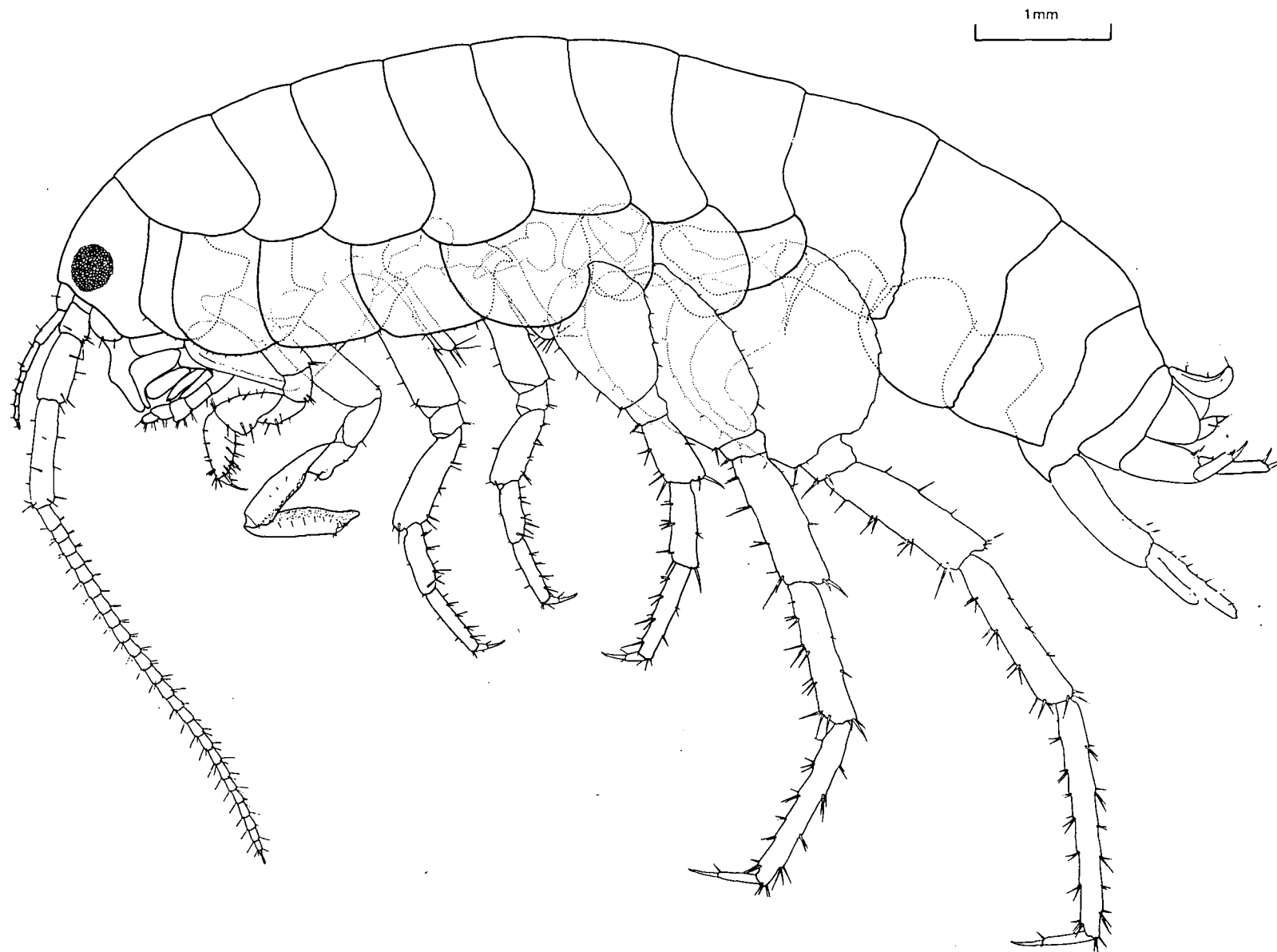


FIGURE 3.55 *Keratroides pyrensis* gen. et sp.n., holotype ♀.

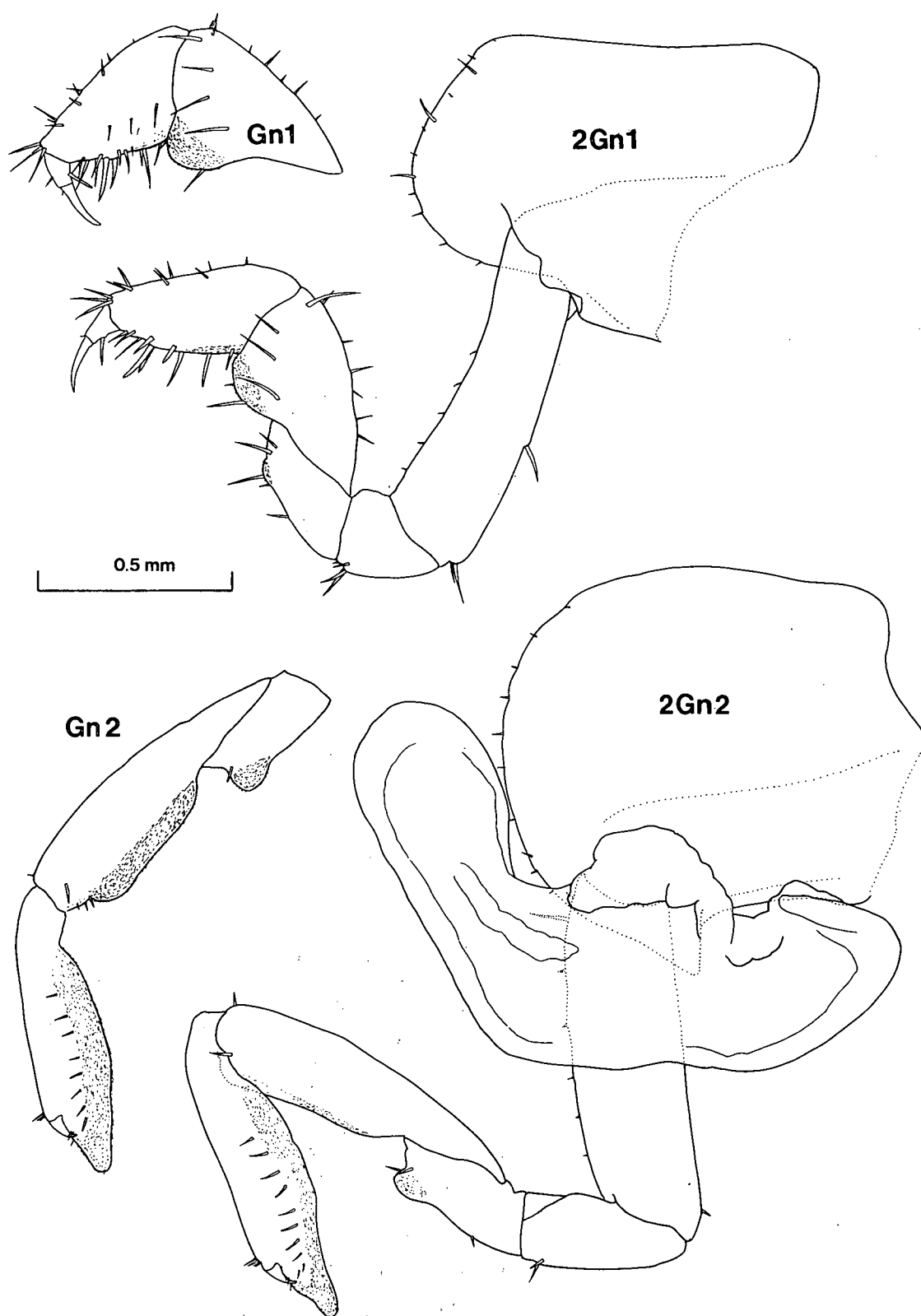


FIGURE 3.56 *Keratroides pyrensis* gen. et sp.n., holotype ♀. 2, allotype ♂.

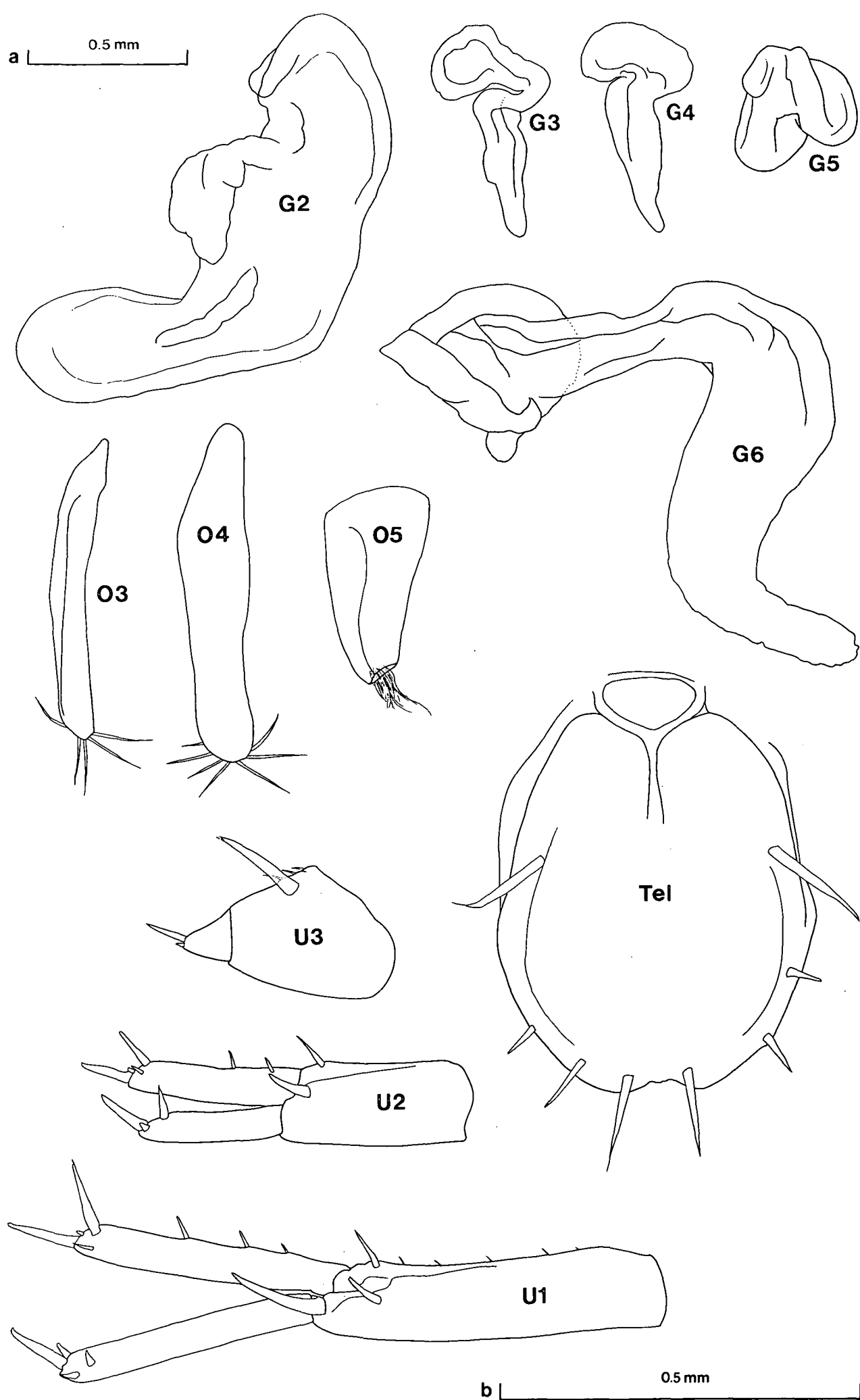


FIGURE 3.57 *Keratroides pyrensis* gen. et sp.n., holotype ♀. Scale a; G2-6, O3-5, U1&2. Scale b; Tel, U3.

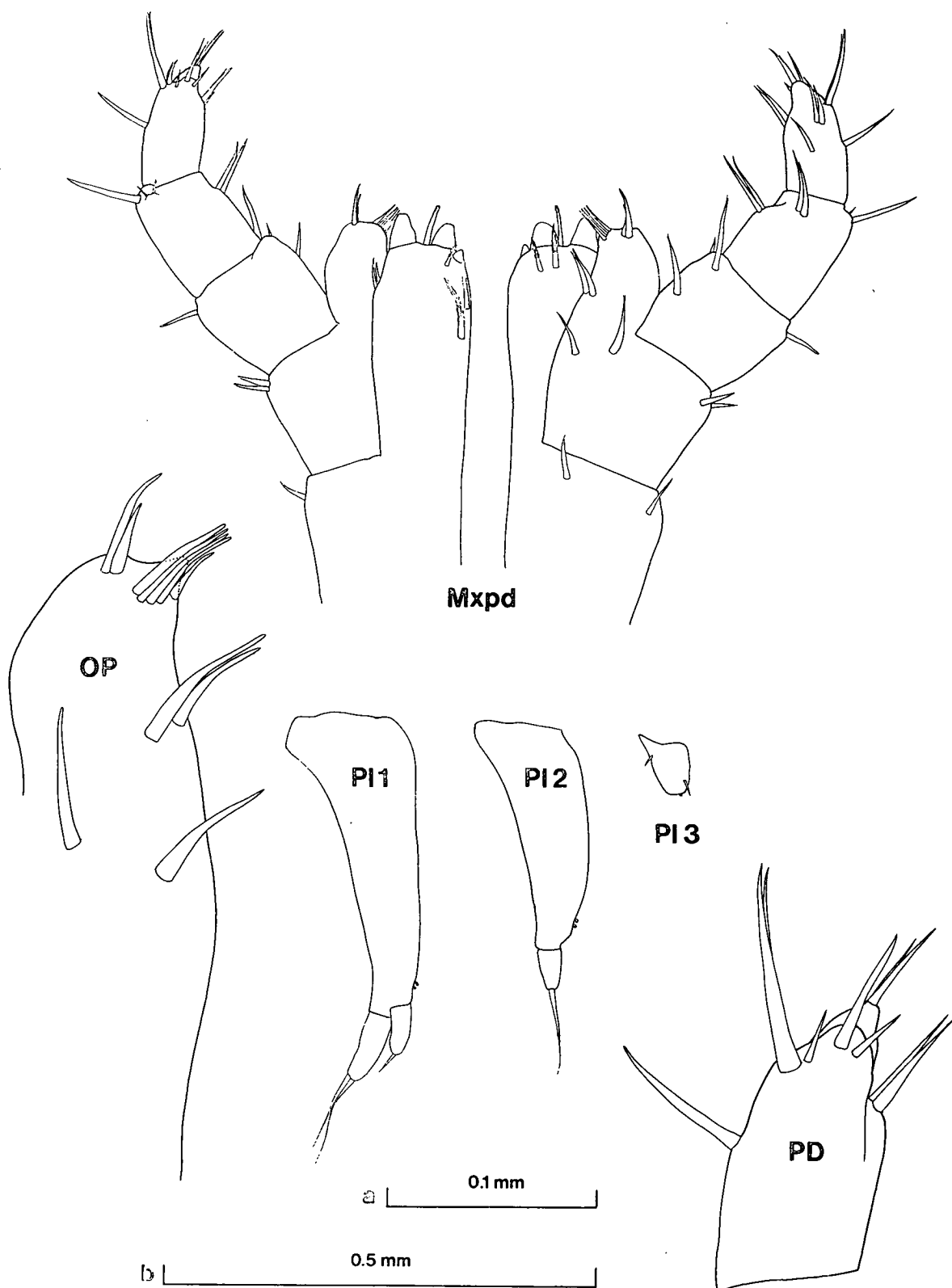


FIGURE 3.58 *Keratroides pyrensis* gen. et sp.n., holotype ♀. Scale a; OP, PD. Scale b; Mxpd, Pl1-3.

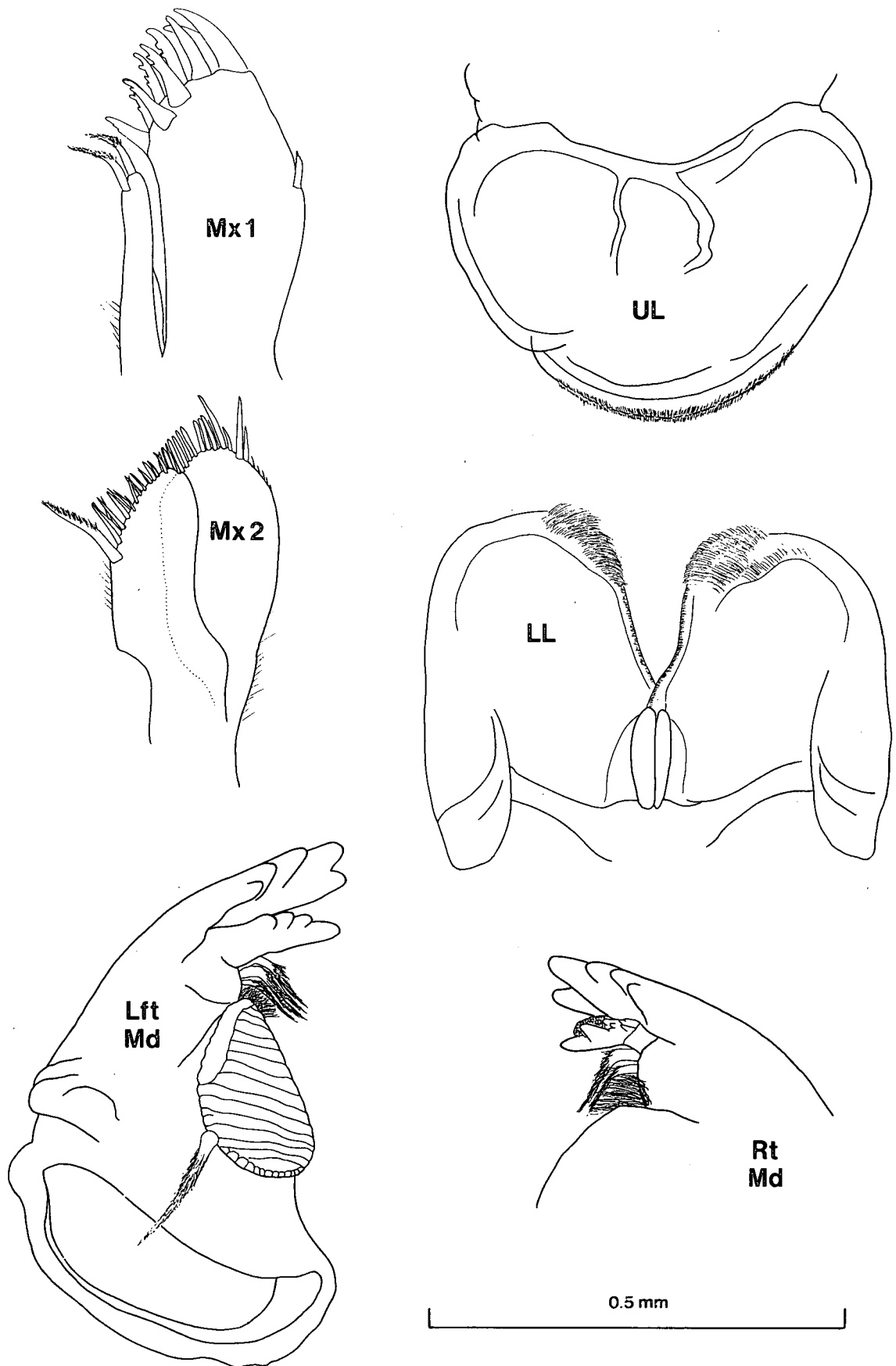


FIGURE 3.59 *Keratroides pyrensis* gen. et sp.n., holotype ♀.

Remarks

Like *K. vulgaris* and *K. rex* sp.n., this species is distinguished by the particular shape of its epimeral plates and sixth peraeopod gills. Males are significantly smaller than females in this species also. The centre of distribution is in NE Tasmania around the Bay of Fires (to which the specific name refers), where it is found in wetter microhabitats than *K. vulgaris*, the only sympatric species. Cysts are commonly found on the gills of *K. pyrensis* sp.n. in this area, similar to those reported on *Orchestiella neambulans* sp.n. (q.v).

Other specimens apparently belonging to *K. pyrensis* sp.n. have been found on Flinders Island, near the Snowy Range and near South Cape Rivulet.

K. vulgaris, *K. rex* sp.n. and *K. pyrensis* sp.n. form a group of similar species distinguished by their vestigial pleopods and anteriorly rounded third epimeral plates. Other species belonging to this group occur on Cape Barren, Flinders and Craggy Islands and in the Hogan Group, but none have yet been found in Victoria.

Keratroides angulosus (Friend)

Figures 3.60 - 3.62

Talitrus (Keratroides) angulosus Friend, 1979 p.91, Figures 1b, 4 and 5.

Types:

Holotype ♀ (ovig.), TMAG, G.1950; Under litter, *Olearia argophylla* stand near Anglers Ck., off Tower Rd., Tooms Lake area. UGR 8413-702229. Coll. JAF, 12.i.1976. Allotype ♂, TMAG, G.1951; same data as holotype. Paratypes, 5 ♂♂, 19 ♀♀ (2 ovig.), 6 imm., TMAG, G.1952.

Other material examined: TASMANIA:

7815-17(1)

7816-17(6), -21(30)

7915-9(3), -15(13), -16(6), -17(1)

8015-4(40), -5(23), -6(6), -7(22), -8(20), -10(42), -11(25),
-14(3), -18(2), -19(1), -21(20), -22(14)

8110-5(35), -6(49), -11(2), -12(51), -21(11), -23(25), -24(9)

8210-5(2), -6(3), -8(19), -11(75)

8215-3(4), -5(66), -6(76), -7(8)

8412-17(11)

8413-1(1), -2(10), -3(15), -5(6), -6(28), -7(1), -9(1), -10(44),
-13(8), -15(33), -16(19), -17(7), -18(8), -19(9), -20(5)

8415-8(4), -12(5), -17(3), -18(44), -19(143)

8514-3(3), 4(84), -5(15), -6(25), -7(2), -8(15), -9(5)

8515-4(1), -5(8)

Diagnosis

A small, unpigmented, soil-dwelling landhopper of the genus *Keratroides*, sexually similar (although males are smaller than females), with short antennae and peraeopods, head dorsally strongly rounded, vestigial pleopods and the third epimeral plate the longest, with sharp front corner, concave below.

Description

Female:

Length 7.1 mm. Head as long as deep, dorsal surface strongly rounded. Eye subcircular, small, about a quarter as wide as head is long. Antenna 1 very short, reaching only to one-third length of distal peduncular segment; flagellum of four segments 3-5, much shorter than peduncle. Antenna 2 short, flagellum of 13 8-16 segments, all bearing four groups of three spines, except proximal three (groups of two) and distal segment (one group of six); peduncle just shorter, distal segment shorter than penultimate two combined.

Upper lip shallow, broad, apically pilose, indentation of right margin marked. Lower lip broad, inner shoulders pilose, sides of central trough lightly pilose. Mandible, incisor 3-toothed, left lacinia bicusperate, large cusp 4-toothed, molar process broad, accompanying setose spine large.

Maxilla 1 broad, inner plate short, distal setae short and strong; outer plate broadening distally to truncate apex, palp near midpoint of outer margin, spine-teeth strong, moderately dentate, innermost leaning inwards, almost lateral.

Maxilla 2, broad, inner plate shorter and just narrower than outer, bearing short, stout spines distally, outer plate with two long sharp spines at the apex, rest of spine-row of strong blunt spines.

Maxilliped, inner plate with inner margin pilose proximally, and three setose spines distally; three terminal teeth present, inner very small, outer tall. Outer plate narrowing distally, apex truncate, bearing spine-groups at the corners (two spines on outer, four on inner corner). Palp slender, bearing a few long spines, fourth segment delimited proximally by a slight shoulder.

Gnathopod 1, coxal plate broad, almost square distally. Segment 2 broadening distally, poorly spined. Segment 4 longer than 3, bearing a

shallow posterior lobe. Segment 5 short, strong, posterior tumescence rounded and deep. Segment 6 just shorter, fairly strongly spined posteriorly, narrowing distally, forming a simple hand with the strong dactyl.

Gnathopod 2, coxal plate subsquare, distal margin evenly rounded, lightly spined; posterior process small, bluntly pointed. Gill large, with anterior and wide posterior extensions; oöstegite entirely absent. Segment 2 linear, lightly spined with two or three larger spines proximally. Segment 4 subequal to segment 3 with large scabrous posterior lobe. Segment 5 equal to segment 6, expanded deeply posterodistally into a scabrous lobe. Segment 6, posterior surface rounded, dactyl well exceeded by apical lobe.

Peraeopods of medium length and stoutness, with larger spines bifid, especially on distal segments. Peraeopod 3 and 4, coxal plate shallow, posterior process prominent, blunt. Gill of medium size, broadening posteriorly; oöstegite short, linear, five [5-7] apical setae.

Peraeopod 5, anterior coxal lobe shallow, lower margin oblique, lightly spinulose, posterior lobe smaller, shallow, posterior margin smoothly rounded. Gill small, convoluted, reduced oöstegite of gill-like texture, posterior margin gently convex, spinulose. Dactyl slender.

Peraeopod 6, posterior coxal lobe deep, smoothly rounded distally; anterior lobe not so deep, rounded distally. Gill long, anseriform, convoluted proximally, then flattened, narrowing distally, with a distal incision. Segment 2 subovate, posterior margin bearing a few spines, distal lobe lacking. Segments 4 to 6 moderately spinose. Dactyl slender, terminal spine long.

Peraeopod 7, coxal plate subrectangular, smoothly rounded posterodistally, with proximal anterior process. Segment 2 not very broad, posterior margin weakly serrulate, distal lobe absent. Segments 4-6 moderately slender and spinose. Dactyl long and slender.

First epimeral plate shallow, posterior margin gently convex, bearing few serrations and spinules. Epimeral plate 2 subsquare, anterior margin

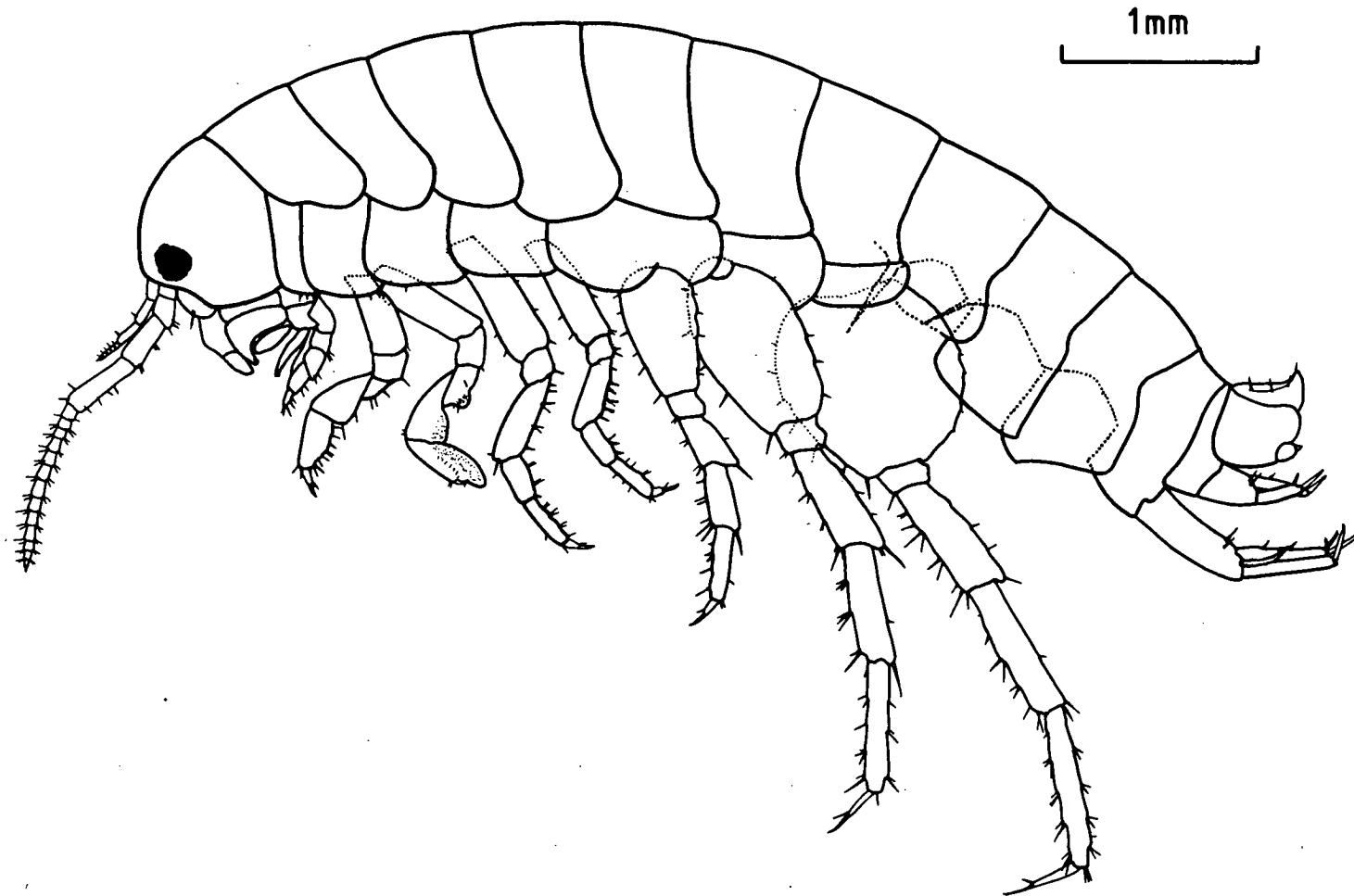


Figure 3.60 *Keratroides angulosus* (Friend) gen.n., holotype ♀.

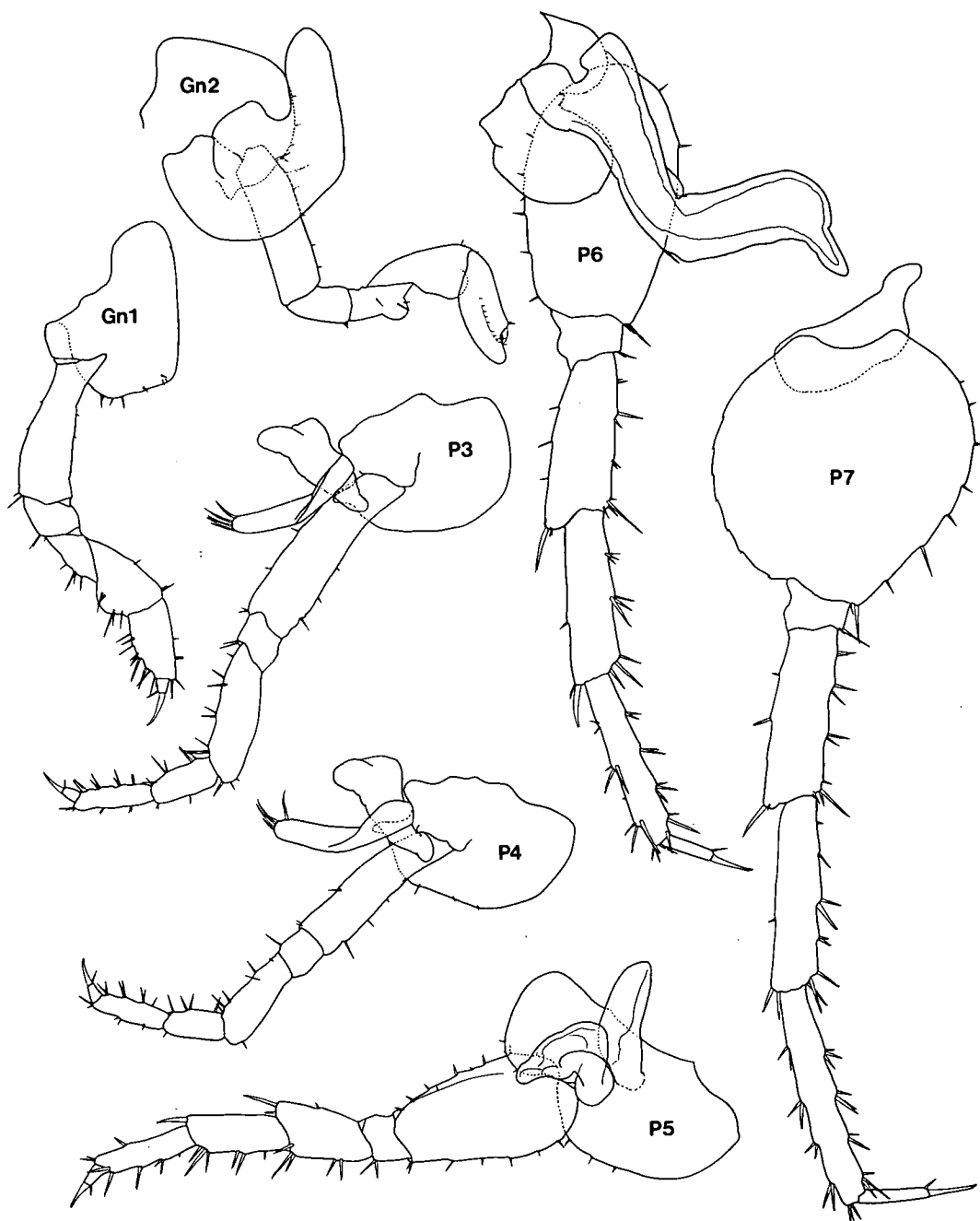


Figure 3.61 *Keratroides angulosus* (Friend) gen.n., holotype ♀, x37.

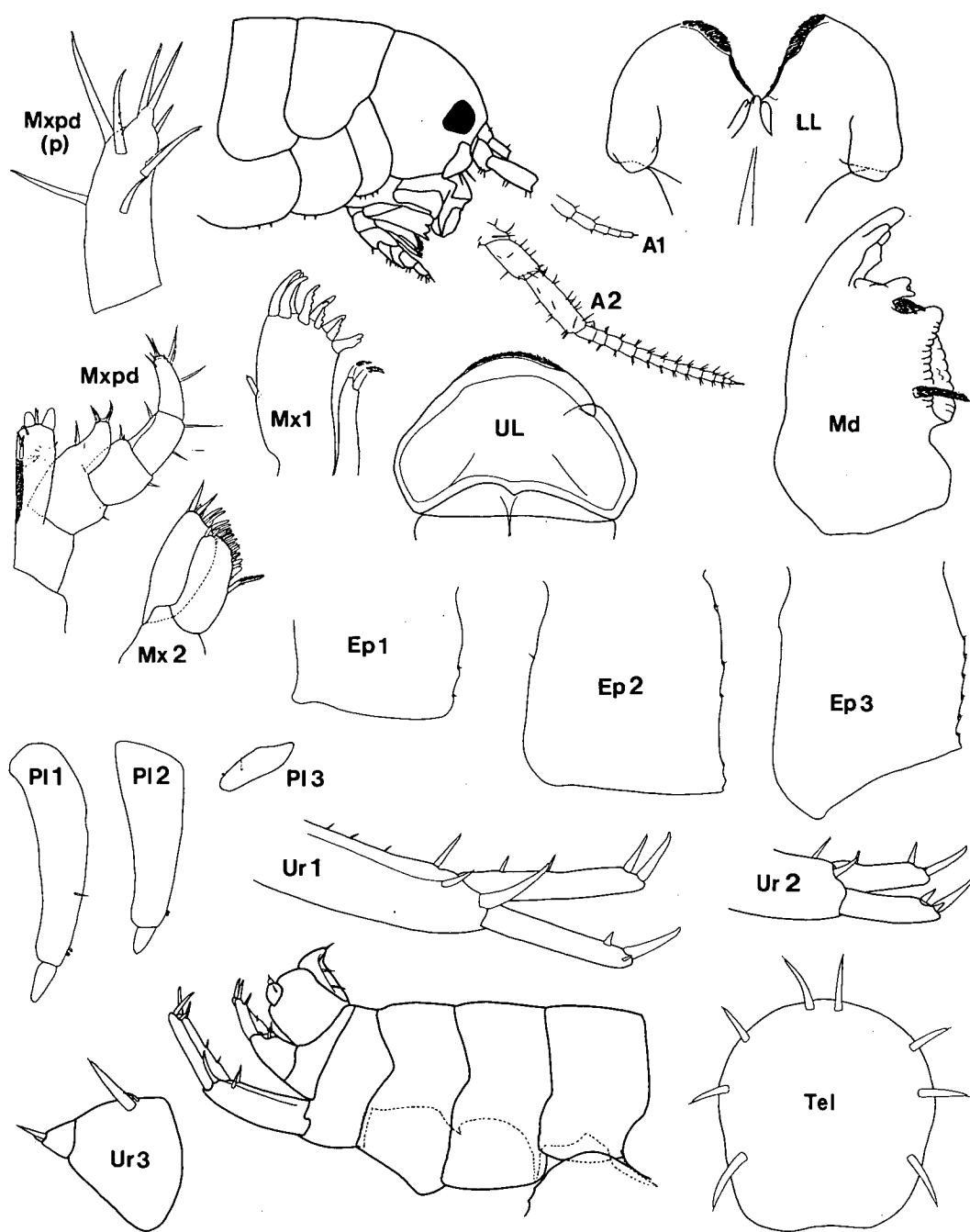


Figure 3.62 *Keratroides angulosus* (Friend) gen.n., holotype ♀. A1&2, Mxpd(p), Ur1-3 as in Figures 3.48 & 49. Ep1-3; epimeral plate 1-3. Head, abdomen, A1&2: x25. UL, LL, Md, Mx1&2: x90. Mxpd: x75. Mxpd(p): x225. P11-3: x125. Ep1-3: x45. Ur1&2: x50. Ur3: x115. Tel: x95.

bearing one small spine, anterior corner rounded. Posterior margin very weakly serrate and spinulose, posterior corner sharp. Epimeral plate 3 deep, well exceeding second plate; lower margin excavate, oblique, anterior corner sharply rounded distally, posterior margin weakly serrate and spinulose distally, proximally smooth.

Pleopods vestigial, peduncle of first short and slender, bearing a spine on the distal half, outer margin concave, inner margin with coupling spines; ramus a terminal segment. Pleopod 2 similar but smaller and without subterminal spine on peduncle. Pleopod 3 reduced to a small stump, bearing one subterminal spine and one coupling spine. [First instar specimens, south coast population: pleopod 1, peduncle short, concave outer margin, inner margin with two coupling spines; two rami present, outer longer than inner, both bearing two long plumose setae, equal in length to peduncle plus respective ramus. Pleopod 2 similar to pleopod 1 but half as long, ramal setae shorter proportionally. Pleopod 3 as in adult.]

Uropod 1, peduncle slender, bearing two subterminal spines, apical spine long, simple; rami slender, inner bearing two marginal spines, outer smooth. Uropod 2, peduncle as long as rami, with two distal spines, inner ramus with one marginal spine, outer ramus smooth. Uropod 3 very small, peduncle short, bearing one large and one very small lateral spine; ramus small, conical, with one small and one minute apical spine.

Telson short, broad, apex broadly rounded, entire; one apical and three [up to four, usually three] marginal spines each side.

Male:

Length 6.3 mm. Like ♀ but bearing paired penes ventrally on peraeonite 7 and lacking oöstegites.

Remarks

Keratroides angulosus differs from other *Keratroides* species in the shape of the peraeopod 6 gills and the third epimeral plates, the telson spination and the simple first gnathopod which is not swollen in male specimens. It is the southern representative of a group of *Keratroides* species including *K. kershawi* which has anteriorly sharp-cornered third epimeral plates. Other species occur in Victoria and on the Kent Group, Craggy, Flinders, Cape Barren, Inner Pasco and Swan Islands in Bass Strait. Several of the Bass Strait islands species have swollen male first gnathopods, as found in *Austrotroides maritimus* sp.n. and *Mysticotalitrus tasmaniae*.

This species occurs in many parts of Tasmania (Chapter 4) where it dwells deeper in the soil than *K. vulgaris* (Section 7.2). It is also less active and has a lower rate of oxygen consumption than that species. As discussed in Chapter 7, *K. angulosus* displays a number of morphological adaptations to the soil microhabitat. In contrast to *K. albus* sp.n., this species appears not to form discrete burrows in the soil. *K. angulosus* is a smaller species than *K. albus* sp.n. and, perhaps more significantly, males are much smaller than females (see Figure 8.1). This supports the view that the larger size of *K. albus* sp.n. is advantageous to burrowing by allowing greater strength to be developed, whereas small size, as in *K. angulosus*, better fits that species to pushing through soil pore spaces and crevices.

Section 3.4 Discussion

Phylogenetic relationships in the Talitridae

A phylogeny for the Talitroidea was proposed by Bulycheva (1957) in which *Talitrus* was derived from the littoral genus *Hyale* and gave rise to the three other supralittoral genera (*Orchestia*, *Talorchestia* and *Orchestoidea*). This hypothesis, however, demands that subchelate gnathopods, which are present in *Hyale*, were lost in *Talitrus*, and subsequently reappeared in the three other genera. Some evidence for regarding *Orchestia* as the most primitive supralittoral group has already been presented (Chapter 2) and in the present work it is suggested that the gnathopod configuration found in this genus is plesiomorphic, and that the configurations found in the other supralittoral genera represent various derived states. This avoids the difficulty of Bulycheva's system.

The lack of close relationship of the supralittoral genera *Talorchestia* and *Talitrus* to landhoppers with similar gnathopod forms has already been indicated (Chapter 2 and Section 3.3). The Tasmanian land amphipods bearing the most features in common with supralittoral groups are those with an *Orchestia*-type gnathopod configuration. Examination of the more detailed published descriptions of terrestrial species shows that this applies elsewhere also. There is thus strong evidence that the *Orchestia* group was ancestral to the majority, if not all of the land amphipods. It is likely, as expressed by Bousfield (1968) and Hurley (1968) that terrestrial amphipods have arisen numerous times from supralittoral species.

Brundin (1966) has emphasised the value of developing plesiomorphic-apomorphic distinctions in character states in the elucidation of phylogeny. Knowing the probable direction of evolution in the Talitridae, we may reverse this procedure and make these distinctions very confidently. In Table 3.2, the expression of a number of characters in supralittoral *Orchestia* and the land amphipods is shown. The supralittoral species [e.g. *Orchestia gammarellus* (Pallas), the type species] are compared with

TABLE 3.2 Development of apomorphic features in the terrestrial Talitridae.

<u>Supralittoral <i>Orchestia</i></u>	<u>Plesiomorphic landhoppers</u>	<u>Apomorphic landhoppers</u>
Antennae		
Short and stout or short and slender.	Short and slender; first antenna	Long and slender; first antenna
First antenna short.	relatively long.	relatively short.
Upper and lower lips		
Deep and narrow, apically bearing	Deep and narrow, apically stiffly	Shallow and broad, apical pilosity
groups of stiff hairs or small spines.	plumose.	less pronounced.
Mandibles		
Strong with many-striate molar.	Not so strong, molar less striate.	Not so strong, molar even less striate.
Maxilla 1		
Narrow, outer plate spines dentate	Narrow, outer plate spines dentate and	Broad, short, outer spines of outer plate less
and more or less longitudinal.	more or less longitudinal.	dentate, inner spines leaning inwards, innermost
		almost lateral.
Maxilla 2		
Narrow, plates of similar width, apical	Narrow, plates of similar width, spines	Broad, plates short inner, narrower than outer,
spines numerous, long and slender.	numerous, long and slender.	spines fewer, short and stout.
Maxilliped		
Broad	Broad	Narrow
Inner plate: distal spine-teeth small,	Inner plate: distal spine-teeth small, sub-	Inner plate: distal spine-teeth grossly unequal,
subequal, often obscured by distal	equal, often obscured by distal plumose	outer two large, not obscured. Bearing few
plumose setae. Bearing numerous plumose	setae. Bearing numerous plumose setae on	plumose setae.
setae on lateral surface and inner margin.	lateral surface and inner margin.	
Outer plate: Rounded, bearing a submarginal	Outer plate: Rounded, bearing a submarginal	Outer plate: apex subacute or truncate, spines in
row of blunt spines on the lateral side.	row of blunt spines on the lateral side.	one or two distal groups.
Palp: Broad, short. Outer marginal spines	Palp: Broad, short. Outer marginal spines	Palp: Narrow, elongate. Normally segments each
short, frequently in groups. Segment 2	short, frequently in groups. Segment 2	bearing single long spine on outer margin. Segments
bearing broad lateral lobe, inner margin	bearing broad lateral lobe, inner margin	2 and 3 narrow, lateral lobes vestigial or absent,
densely armed with spines. Segment 3	armed with a group of numerous spines. Seg-	bearing one or a few long slender spines on inner
with a broad laterodistal lobe, which	ment 3 with a broad laterodistal or lateral	margin. Segment 4 distal, often partly fused to
completely masks small rounded fourth	lobe, completely or partly masking the small	segment 3.
segment, inner and distal margins densely	fourth segment, inner and distal margins	
spined.	spinose.	

<u>Supralittoral Orchestia</u>	<u>Plesiomorphic landhoppers</u>	<u>Apomorphic landhoppers</u>
Gnathopod 1.		
Sexes different.	Sexes different.	Sexes similar.
Inner shelf well-developed, spinous.	Inner shelf weak, few spines.	Inner shelf vestigial, no spines.
Scabrous lobes present.	Scabrous lobes present.	Scabrous lobes small or absent.
Gnathopod 2		
Sexes different.	Sexes different.	Sexes similar.
♀ segment 2 broad, (forming accessory oöstegite ?), ♀ segment 6 short, broad.	♀ segment 6 short, ♀ segment 2 broad.	♂, ♀ segment 6 elongate, slender.
♂ segment 2 broad, strong.	♂ segment 2 broad, strong.	♂, ♀ segment 2 narrow.
♂ hand heavy, strong.	♂ hand expanded usually very strong.	♂ hand mitten-shaped like ♀.
Peraeopods (3-7)		
Stout, segments strong.	Short, slender.	Long, slender.
Sexual differences.	No sexual differences.	No sexual differences.
Oöstegites		
Four pairs, broad, long, numerous apical and marginal setae.	Four pairs, broad or narrow, apical and marginal seta present.	Three or four pairs, slender, long or short apical setae only. Posterior pair short, non-setose, held laterally across ventral surface.
Gills		
Simple, sac-like, equal, of medium size.	Simple, sac-like, equal, small to medium size.	Anterior and posterior gills large, others small. Gn 2 gill with large anterior extension. Pr 6 gill anseriform, or convoluted. Pr 3-5 gills convoluted.
Pleopods		
Long, broad, equal, biramous, setose.	Long, slender, equal or smaller posteriorly, biramous, setose.	Short, broad and biramous or reduced to stumps with vestigial or no rami. Segmentation of rami, plumose setae absent.
Epimeral plates		
Subsquare, subequal, posterodistal corner slightly produced behind.	Subsquare, subequal, posterodistal corner slightly produced behind.	First plate reduced, second and third variously enlarged and distally modified.
Uropods		
Short, stout, no interramal spine, bearing numerous short stout spines on peduncle and margins of rami. Ur 3 ramus relatively long, laterally spined.	Slender, interramal spine present, bearing slender spines on peduncle and margins of rami. Ur 3 ramus relatively long, laterally spined.	Long, slender, interramal spine large, bearing slender spines on peduncle and margins of inner rami only: apical spines on rami elongate. Ur 3 small, ramus very short, apical spines only.
Body		
Large, fairly stout, laterally compressed	Small, fairly stout, laterally compressed.	Large, slender, laterally compressed.
Genera		
<i>Orchestia</i> .	<i>Agilestia</i> , <i>Orchestiella</i> , <i>Tasmanorchestia</i> . Some features of <i>Austrotroides</i> and <i>Neorchestia</i> .	<i>Keratroides</i> , <i>Arcitalitrus</i> , <i>Mysticotalitrus</i> . Some features of <i>Neorchestia</i> , <i>Austrotroides</i> .

the fully terrestrial Tasmanian species morphologically closest to them ("plesiomorphic landhoppers") and also with species divergent from them ("apomorphic landhoppers"). Although the well-described species *O. gammarellus* is used in this comparison, an investigation has shown that a similar Tasmanian beach-hopper, *O. marmorata* Haswell, displays the same features.

From Table 3.2, therefore, it is possible to decide which character states are apomorphic. It is important to note that the progression away from the shore-hopper facies does not occur steadily through a neat series of generic groups. In fact it is apparently happening in a parallel fashion, simultaneously, in different groups. For example, if *Neorchestia* and *Austrotroides* are compared, it is seen that while *Austrotroides* retains plesiomorphic mouthparts and urosome, its gill and pleopod configurations are amongst the most apomorphic, and sexually similar gnathopods have already appeared. On the other hand, *Neorchestia* possesses sexually dimorphic gnathopods and biramous, though reduced, pleopods while the mouthparts, gills and oöstegites show substantial apomorphy.

In the case of the terrestrial Talitridae, apomorphic character states represent the result of adaptation to terrestrial environments. Amongst the Tasmanian species, and those of other areas which have been sufficiently well described (e.g. Bousfield, 1971; Friend in MS), sexually similar gnathopods are found only in species displaying other apomorphic features, such as reduced pleopods, unequal and complex gills, and reduced lateral lobes on maxilliped palps. It may be concluded, therefore, that the possession of this gnathopod form by a species indicates substantial adaptation to land. It appears also that sexual dimorphism of gnathopods has been lost a number of times. These conclusions have important implications for an understanding of the zoogeography of the land amphipods of the world (Section 4.4).

It follows from the above arguments that both the sexually dimorphic and sexually similar groups of terrestrial Talitridae are probably

polyphyletic. This conclusion indicates the danger of hastily proposing relationships between genera. A multiplicity of characters should be used in drawing phylogenetic conclusions. It is important not to mistake as evidence of relationship, features which have developed convergently as the response of the common marine genome to the common terrestrial selection pressures.

In the opinion of Bousfield (1968), there is a total number of 200-500 species of terrestrial Amphipoda in existence; the number described now is about 90. The detailed description and redescription of species from other areas is desirable to allow more meaningful discussion of phylogeny.

CHAPTER FOUR

DISTRIBUTION AND ZOOGEOGRAPHY

Section 4.1 Introduction

The study of zoogeography involves a synthesis of information relating to the history, environment and biology of a group in order to explain its distribution. A zoogeographical explanation, however, is merely the most probable hypothesis available; it is not an empirical scientific system *sensu* Popper (1959) as its falsifiability is not possible.

The main questions to which answers will be sought in this chapter are

- 1) how are the various Tasmanian terrestrial amphipod species distributed?
- 2) how did this distribution come about?
- 3) what does this information reveal about the distribution and origin of terrestrial amphipods generally?

The world distribution of land amphipods has not been reviewed since the work of Hurley (1968), and since then much new information emerged. The overall picture is somewhat unclear due to the increasing presence of artificially introduced species in various parts of the world. An attempt will be made to rectify this situation in the following pages.

World distribution of the terrestrial Talitridae

Terrestrial amphipods (excluding *Niphargus talikhadzei* Levushkin - Chapter 1) are a tropical and southern hemisphere fauna (Hurley, 1968). There are several exceptions to this pattern, which may be seen from the map of the known distribution in Figure 4.1, based on records listed in Appendix II. Recent introductions do not appear on this map; records from the western U.K., U.S., European and American hothouses and Brazil (de Castro, 1972), are therefore omitted. Examination of the actual

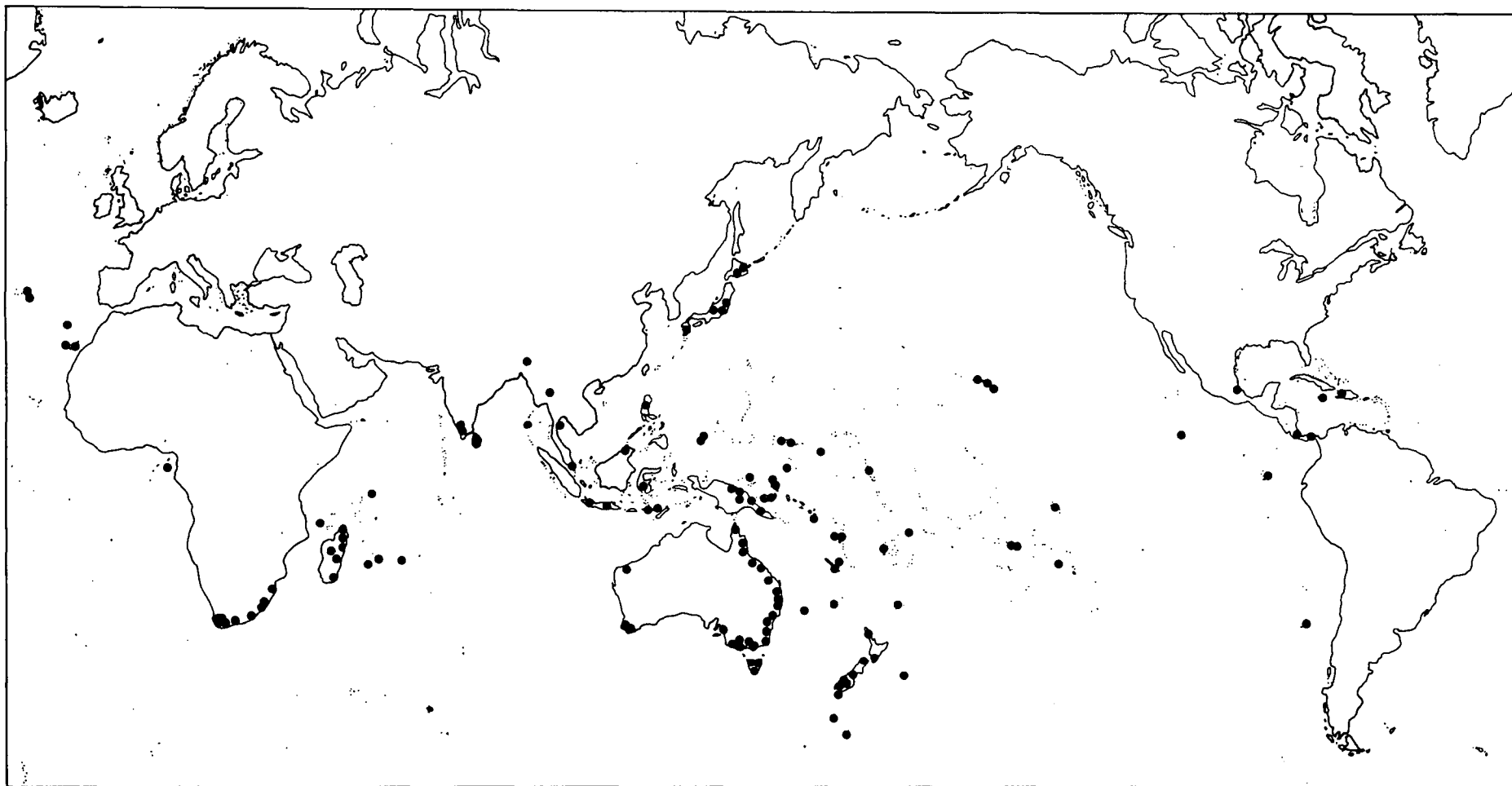


Figure 4.1 Recorded distribution of terrestrial amphipods with localities in some unpublished records. References listed in Appendix II.

species recorded, especially in more recent work, gives the impression of strong endemism amongst the landhoppers of the world. Records of widespread species are being more frequently attributed to introduction by man (Dahl, 1967; de Castro, 1967; Bousfield and Howarth, 1976; Biernbaum, 1980). A discussion of five species for which records appear from several different parts of the world follows.

Widespread species

a) *Arcitalitrus dorrieni* (Hunt)

The spread of this species in areas of the western British Isles possessing mild climates, facilitated by the introduction and transfer of exotic plants, has been well documented (Hunt, 1925; Rawlinson, 1937; Hurley, 1955; Ingle, 1958; Murphy, 1974, 1975; Richardson, in press). There has been some uncertainty about the identity of this species (Hurley, 1955). Recent examination of a large quantity of material from eastern Australia as part of the present study has revealed the presence of a number of species closely related to *Talitrus dorrieni* Hunt, grouped above as the genus *Arcitalitrus* (Chapter 3). Comparison of specimens with the drawings of *Talitrus dorrieni* by Hunt (1925) and *Talitrus sylvaticus* by Sayce (1909) shows that these workers were dealing with distinct species which are sympatric in New South Wales and southern Queensland today. Landhoppers from a garden in Wellington, N.Z. (kindly collected by M. Hine) closely resemble specimens of *A. dorrieni* from N.S.W., and Hurley's drawings (1955) of "*Talitrus sylvaticus*". I have also examined material from Cornwall and the Isles of Scilly (U.K.) and Norfolk I. (Pacific Ocean), all of which contained *A. dorrieni*. Whether the British introductions were from eastern Australia, New Zealand or Norfolk I. is not known, but as *Arcitalitrus* is obviously an Australian group, and accepting the tendency of landhoppers to be endemic to restricted areas, we must conclude that the New Zealand and Norfolk I. populations almost certainly originated as introductions from Australia.

b) *Arcitalitrus sylvaticus* (Haswell)

Haswell's original description of this species (1880) gives very little useful morphological information. Neither Sayce's redescription of *Talitrus sylvaticus* (1909) nor Hunt's description of *T. dorrieni* (1925) contain significant points of difference from Haswell's brief diagnosis and poor drawings. Haswell's original specimens are apparently lost, although two specimen lots exist, both labelled as types of *Talitrus sylvaticus*, and both bearing the same registration number from the Australian Museum (G5423). One of these, a single specimen belonging to *A. dorrieni*, was found in the Australian Museum with an old label, apparently in Haswell's writing "Talitrus sylvaticus Hasw. 391. Elizabeth Bay. In a garden". Other labels with this specimen indicate that four specimens were loaned in 1938 to Dr. K. Sheard, South Australian Museum, but only one was returned, in 1951. The other lot was found in the collections of the South Australian Museum, and contained four poorly preserved specimens of *Arcitalitrus sylvaticus* (as described by Sayce). All labels with these specimens (no locality given) are apparently more recent than Haswell, although none were written by Sheard.

Hurley (1955) used the information from Sheard that the old specimen of Haswell's agreed with *A. dorrieni*, in synonymising *A. sylvaticus* and *A. dorrieni*. The facts related above explain how Hurley made his mistaken synonymy, but throw no light on whether Haswell had *A. dorrieni* or *A. sylvaticus*, as redescribed by Sayce, the only two native species found in the Sydney area.

For the sake of convenience, it is best to support Sayce's assumption that the species also occurring in his State, Victoria (*A. dorrieni* does not), was the one Haswell described. Certainly it is likely that Haswell's mention of landhoppers from Rooty Hill, 50 km inland, refers to *A. sylvaticus* (Sayce), because this species lives in drier habitats than *A. dorrieni*, such as those in western areas of the Sydney Basin.

Although *A. sylvaticus* has a large recorded distribution outside Australia, most of the material has been found to belong to *A. dorrieni* or *Talitroides topitotum* (Burt) (= *Talitrus pacificus* Hurley; see Hurley, 1955). The only genuine introduction of the species appears to be to California (Bousfield and Carlton, 1967).

c) *Talitroides topitotum* (Burt) (= *Talitrus pacificus* Hurley)

I have examined numerous specimens referable to this species from Madagascar, Norfolk I., Hawaii, New South Wales and Queensland and must conclude, with Bousfield and Howarth (1976) that its widespread distribution is owed to accidental introduction by man. Its three descriptions [as *Talitrus (Talitropsis) topitotum* Burt, 1934, from Ceylon, *Talitrus decoratus* Carl, 1934, from India and *Talitrus (Talitroides) pacificus* Hurley, 1955, from Norfolk I.] are due to this wide tropical occurrence. On the basis of these synonymies, records of this species are from Mauritius, Madagascar, Reunion, the Comoro Is., Sri Lanka, Southern India, the Azores, Madiera, New South Wales, the Hawaiian Is. and California, omitting hothouse occurrences. I have also found specimens in collections from Queensland. Further discussion is included under *T. alluaudi*.

d) *Talitroides alluaudi* (Chevreux)

This small species is closely related to *T. topitotum* and shares its tendency to be easily transported by man (Bousfield and Howarth, 1976), judging from its wide distribution and affinity for gardens and hothouses (Vader, 1972). It has been recorded from the Azores, the Canary Is., Madagascar, the Seychelles, the Hawaiian Is. and the Gambier Archipelago. I have examined specimens from Madagascar, supporting the records by Chevreux (1901) despite doubt by Ruffo (1958) of their validity. Other specimens have come to hand from the New Hebrides, Lord Howe I., the Pelbara (Western Australia) and Sydney, New South Wales.

The distribution of *T. alluaudi* and *T. topitotum* is becoming increasingly wide, on the evidence of Dahl (1967), de Castro (1972) and

Bousfield and Howarth (1976), to the extent of displacing the native landhoppers. However, the place of origin of these species is not obvious. Circumstantial evidence will be gained when other *Talitroides* (s.str.) species are found at a locality where both *T. alluaudi* and *T. topitotum* occur.

e) *Orchestia anomala* Chevreux

This species differs from the four above in that it is found in the supralittoral zone as well as in forest litter. Its presence "on low islands and atolls of the Indo-Pacific region, from the Seychelles and Indian Ocean islands, throughout Indonesia, Melanesia (Bismarcks, Solomons) to Micronesia" (Bousfield, 1971) implies that it has been transported freely throughout these tropical areas on drifting plant matter. Unlike the fully terrestrial species, *O. anomala* must be able to survive the immersion which would almost always occur during long ocean voyages. This distribution stretches to the western limits of the Indian Ocean; Ruffo (1958) recorded *O. anomala* from the Comoro Is., while one individual is present in a sample from Madagascar in my own collection. The implied ability of this species to cross oceans frequently by natural means sets it apart from most landhoppers in zoogeographical considerations.

Natural distribution of fully terrestrial species

To gain a true appreciation of the distribution of landhoppers, uninfluenced by man, it is necessary to ignore certain records, even in the Indo-Pacific region. Some records consist only of the occurrence of one or more of the species above, with no endemic species present; we may remove the effect of man's agency and of *O. anomala* by omitting those records from our picture of the world distribution. In fact, the only localities which would then be omitted are the following: the Seychelles, Madagascar, the Comoro Is., Madiera, Norfolk I., Mangareva (Gambier Archipelago), and the Pelgara (Western Australia).

This changes the general picture of the world landhopper

distribution very little from that shown in Figure 4.1, on which the following discussion will be based.

Note: It has been assumed (Hurley, 1968; Bousfield, 1968) on the basis of the lack of records, that terrestrial amphipods are absent from South America. It is suggested that it is too early to draw this conclusion, particularly in the light of two interesting facts. One is the presence of endemic landhoppers in Jamaica (Hurley, 1959), Barro Colorado I., Canal Zone (Hurley, 1968) and Mexico (specimens from E.L. Bousfield). The other is a reference in a study of terrestrial arthropods occurring between Santiago and Valparaiso, Chile, in which amphipods were caught in pitfall traps, apparently set well away from water, at two different inland localities (Noodt, et al., 1962). Land amphipods were apparently not collected, however, during the Royal Society Expedition to southern Chile in 1958-1959 (Kuschel, 1960).

Theories of terrestrial amphipod distribution

Hurley (1968) outlined four hypotheses to explain the world distribution of terrestrial amphipods:

- a) Continental drift
- b) Distribution along continental margins and island arcs
- c) Local origins from littoral species
- d) Distribution by man.

He proposed that the last three hypotheses were likely to be important in varying degrees, but discounted continental drift because of the lack of South American records, and his belief in the relatively recent origin of landhoppers.

In considering land amphipod distribution, Bousfield (1968) treated the sexually dimorphic and the sexually similar species separately. The first group, he felt, owed their origins to development of terrestrial species from local supralittoral amphipods in many different areas. On the other hand, he suggested that continental drift was a suitable explanation

for the distribution of the sexually similar group. He drew attention to three different, geographically separated groups of species in the second group, occurring in the following regions:

- a) Madagascar and Southern India (presumably *Talitroides alluaudi* and *T. topitotum*)
- b) Tasmania, south-west Western Australia and South Africa
- c) Queensland, New Guinea and Melanesia (now known as *Brevitalitrus* Bousfield, 1971)

Hurley (1975a) updated his information on world distribution and proposed subgeneric division of the sexually similar group, noting affinities which corresponded to geographic areas. He remarked that this group was restricted to Gondwanaland localities marginal to the Antarctic plate during the Jurassic. Hurley therefore postulated a single origin for the group, which occurred after the separation of South America, South Africa and Antarctica.

A severe limitation to the study of the zoogeography of landhoppers is the poor state of knowledge concerning their affinities. As most records and descriptions deal with only one or two species, comparison between faunas is difficult. Hurley (1975a) recognized some relationships amongst the sexually similar species, working mostly from the literature. There have been few treatments even of regional faunas, exceptions being those of K.H. Barnard (1940), Hurley (1957), J.L. Barnard (1960) and Bousfield (1971). Furthermore, even these few studies were limited by the small amount of material available. Hurley's work on the sexually dimorphic species of New Zealand (1957) is the only regional study of this large group, and this lack of synthesis has made any conclusion about origins difficult. It is hoped that the present intensive study of a regional fauna will contribute sufficiently to the available knowledge to allow significant progress in this area.

Section 4.2 Environments, present and past

Tasmanian environments today

Physical Description

Tasmania is an island about $67\,000\text{ km}^2$ in area which lies between latitude $40^{\circ}30'S$ and $44^{\circ}S$ and longitude $144^{\circ}30'E$ and $148^{\circ}30'E$. There are many offshore islands, some of which are relatively large; these are shown in Figure 4.2, with a number of other localities mentioned in the text. Tasmania is separated from south-eastern Australia by Bass Strait, a shallow marine transgression over 240 km wide and up to 85 m deep. A chain of island groups occurs on the eastern side of Bass Strait, including the Furneaux, Kent and Hogan Groups, with several small islands near Wilsons Promontory, Victoria. On the western side, there are few very small islands; King I. is situated about halfway between Cape Grim (N.W. Tasmania) and Cape Otway (Victoria). The Hunter Group is much closer to Tasmania and constitutes the only other significant land on the western side of Bass Strait. The Maatsuyker Group comprises several small islands off the south coast, while Bruny, Maria and Schouten Is. are larger islands off the east coast, separated by shallow water from mainland Tasmania.

The main island, especially the western half, is mountainous, the highest peak reaching 1617 m. The Central Plateau (over 1000 m) and the mountains of the north-east are separated by the relatively low-lying Midlands graben, while the coastal plains are generally narrow, except in the north and north-east.

Geologically complex, the island may be broadly divided into the "fault structure province" of the centre, east and south-east, and the "fold structure province" of the west and north-east (Davies, 1965). The fault structure province is made up of mostly Permian and Triassic sediments with massive dolerite intrusions. These layers are roughly horizontal, but the formation of grabens in the central north and south-east has caused strong drainage patterns to emerge. The fold structure province is made up

of the pre-Carboniferous basement rocks which have undergone folding and some intrusion by granite. The folding in the west runs roughly north and south, forming a number of low ranges with interposed depositional plains.

Climate

The climate of Tasmania is temperate maritime (Bureau of Meteorology, 1979). Temperatures are influenced by topography, but January mean maximums vary between 18° and 23° and July mean minimums between -1° and 5° . Daily temperature ranges average between 8° and 12° , depending on locality. As the island lies in the path of the "Roaring Forties" (a westerly air stream), rainfall is year-round, with a winter peak. The elevated nature of western Tasmania causes a strong west-east decrease in precipitation. Average annual rainfall varies between 550 mm and 3600 mm; the distribution of this is shown in Figure 4.2.

Vegetation and terrestrial amphipod habitats

Jackson (1965) has distinguished five broad vegetational types in Tasmania; rainforest, sclerophyll forest, moorland, sedgeland and coastal heath. The first two of these appear to support most of the landhopper populations in Tasmania, while the other three seem to be marginal habitats. Figure 4.3 shows the distribution of rainforest, sclerophyll forest, and the three non-forest types, grouped together.

Rainforest occurs mainly in the western, high rainfall area with an outlier in north-eastern Tasmania. This forest type is a mosaic of different communities, intergrading according to the conditions prevailing at each site.

According to Jackson (1965, 1968), much of the area climatically suited to rainforest carries other communities because of mineral and fire frequency status. An extreme case is that of Button-grass (*Gymnoschoenus*) sedgeland (which occupies most western areas in the non-forest category, Figure 4.3), where poor soils and frequent burning prevent forest development.

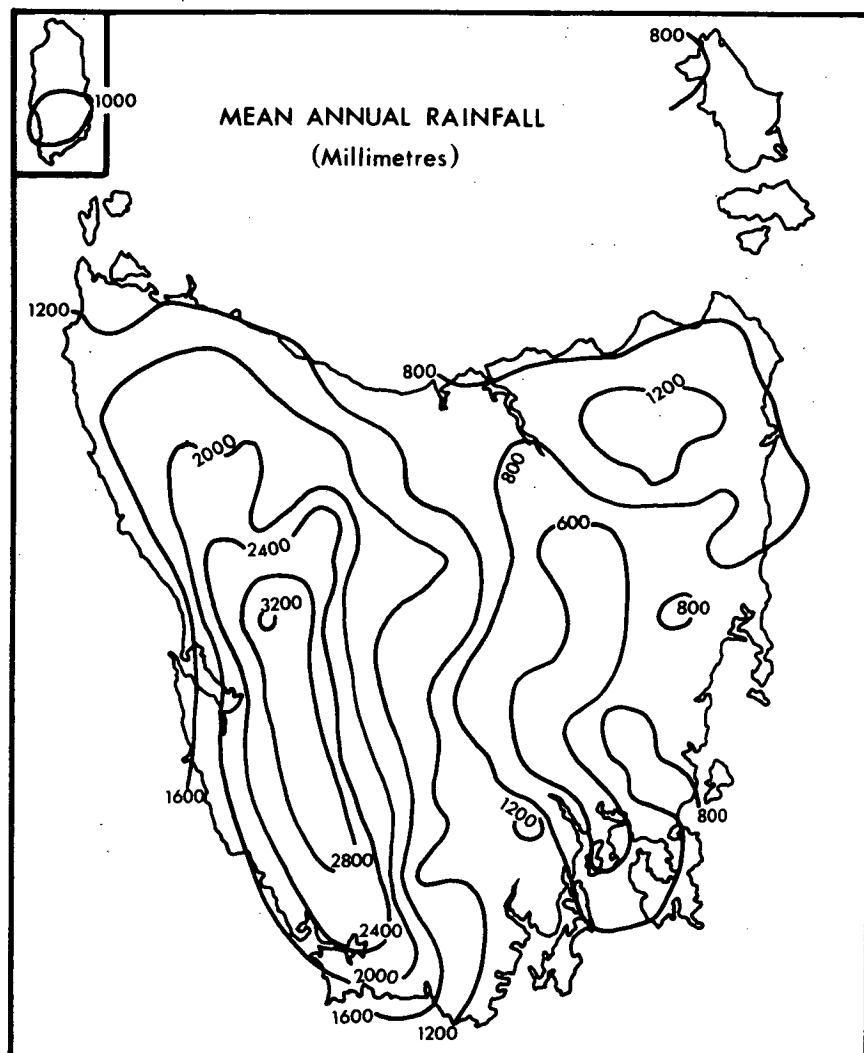


Figure 4.3 Rainfall map of Tasmania (from Bureau of Meteorology, 1979).

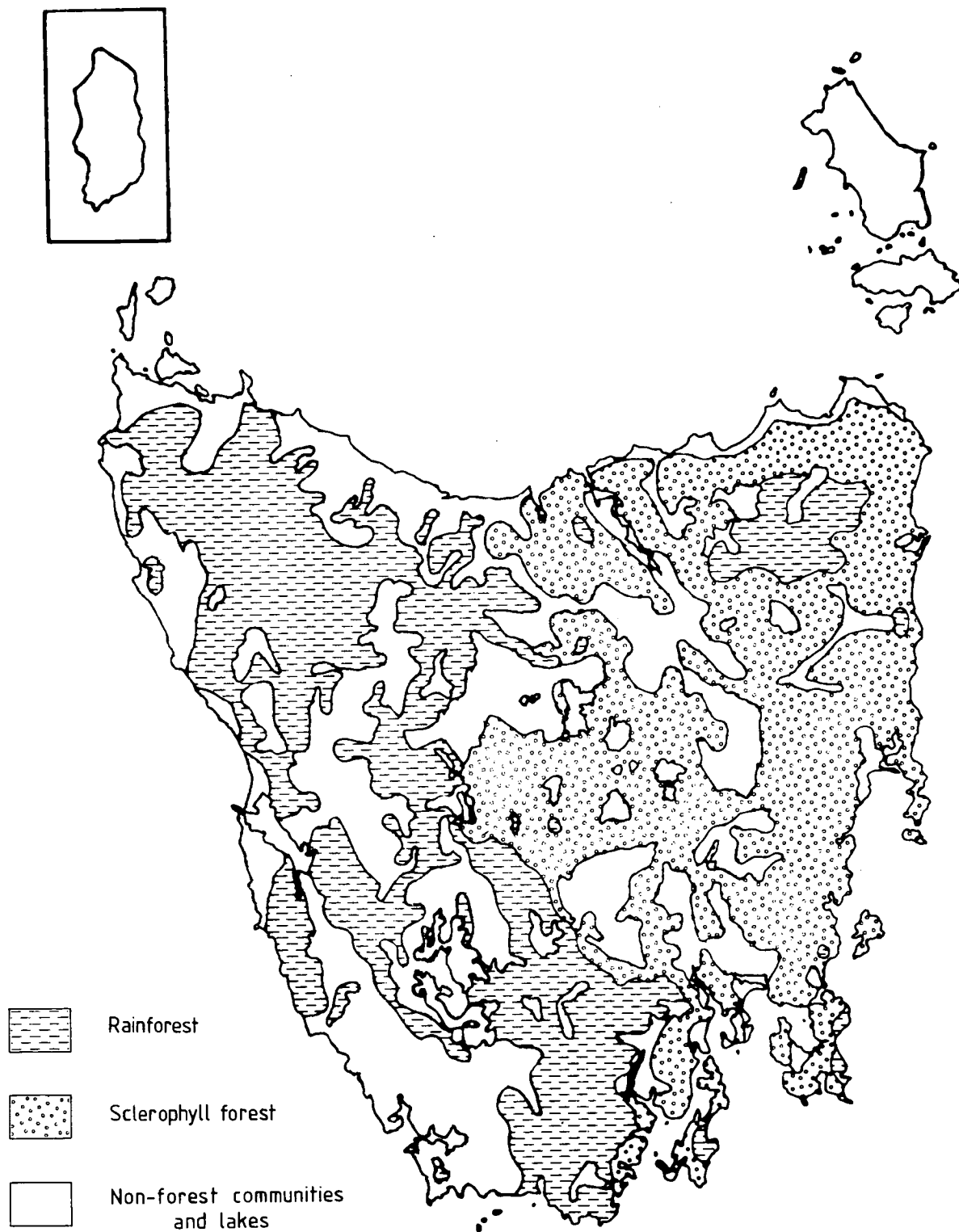


Figure 4.4 Distribution of forest in Tasmania (after Jackson, 1965; adapted from Thomas, 1978).

Another important fire-mediated subclimax is *Leptospermum* scrub and woodland, which is usually poorly drained, and provides habitats to which two particular landhopper species seem adapted. At low fire frequencies, but low mineral status, *Nothofagus* climax rainforest gives way to Horizontal (*Anodopetalum biglandulosum*), which forms a tangled mass of interwoven stems at understorey level. Progressively better soils support Celery-top Pine (*Phyllocladus aspleniifolium*) and then Sassafras (*Atherosperma moschatum*) dominants, before the climax Myrtle (*Nothofagus cunninghamii*) rainforest, which occurs on good soils. These last three forest sub-types have almost closed canopies and litter layers with a mat of rootlets above the mineral soil; the litter/soil interface, an important microhabitat for many amphipod species, is not well developed. In wet areas with good soils and intermediate fire frequency, eucalypts occur above rainforest subdominants. This mixed forest provides a heterogeneous litter which is well colonized by landhoppers. All forest types mentioned above are grouped as rainforest in Figure 4.3.

The other major forest type in Tasmania is sclerophyll forest, which occurs mainly in the east. It is dominated by eucalypt trees and the structure is closed with a thick understorey in wet situations, tending to be more open with the understorey sparse or absent as conditions become drier. This forest type provides suitable habitat for amphipods, except where low rainfall and open structure allow desiccating conditions to prevail. Even in these dry sclerophyll areas, gullies tend to support thicker vegetation, higher humidity and amphipod populations.

It should be pointed out here that field work in parts of Tasmania is greatly restricted by lack of accessibility. Most of the south-west quarter of the island (and large areas further north) is uninhabited wilderness, only partly penetrated by roads. Most localities sampled in that region during the present study were therefore reached on foot. Helicopter transport to some areas was available, however, during an environmental survey of valleys threatened by a proposed hydro-electric power generating

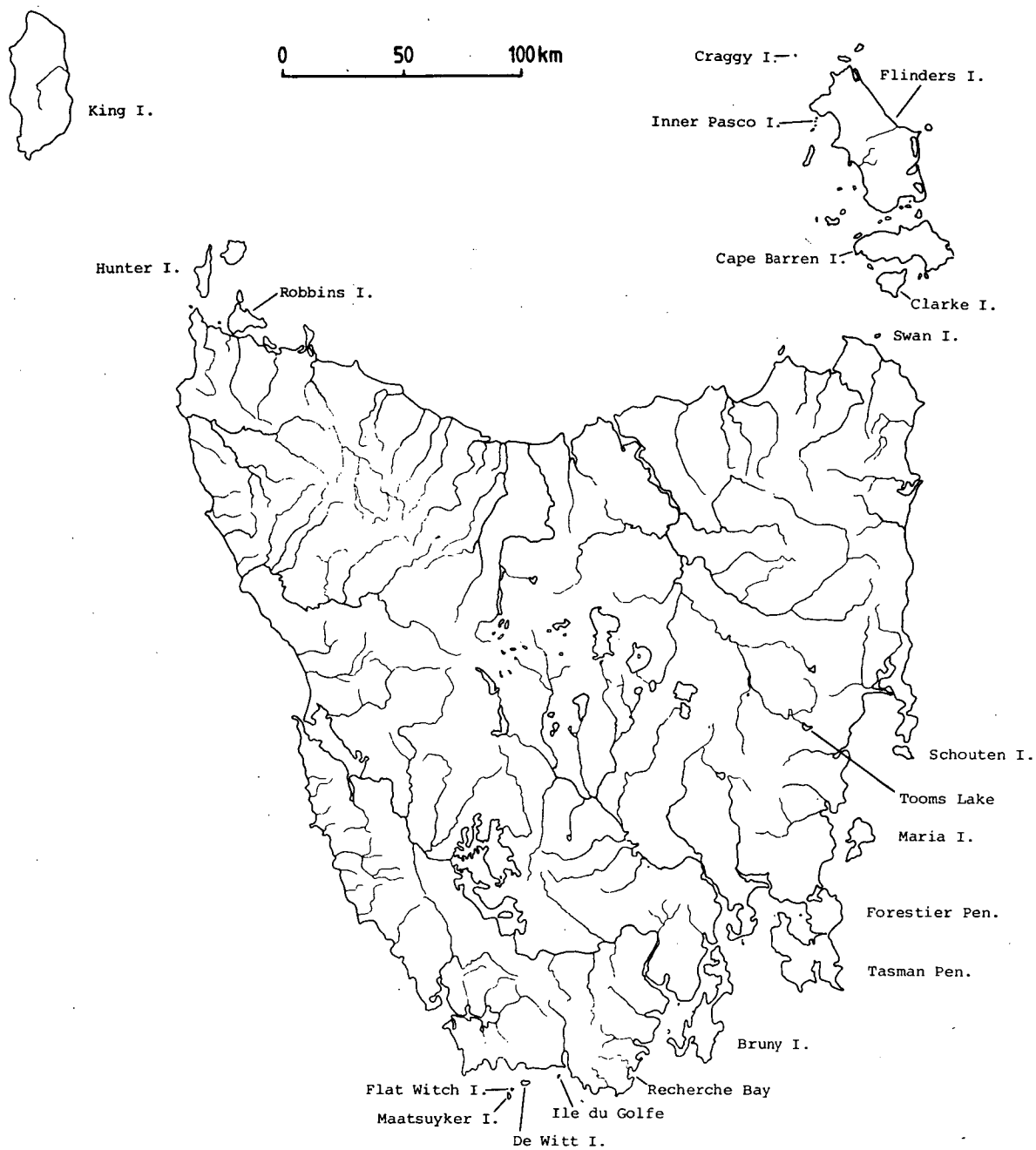


Figure 4.2 Location of some Tasmanian geographical features mentioned in the text.

scheme. Access to other parts of the State is somewhat easier, with the exception of the smaller offshore islands. Expeditions to these islands, especially those off the south coast, were severely limited by weather conditions and cost. The important contribution to this study by Mr. John Whinray, who made numerous collections in very poorly accessible areas of eastern Bass Strait, is gratefully acknowledged.

Land connections

The depression between mainland Australia and Tasmania which, when flooded, forms Bass Strait, is a NW-SE trending, elliptical graben which originated during the separation of Australia and Antarctica at about 65My BP (Griffiths, 1971). This area was flooded between the late Oligocene and the end of the Miocene, and again from the Pliocene until the Pleistocene. During the Pleistocene, five glacial phases apparently occurred in other parts of the world (Ericson and Wollin, 1968) and sea-level changes associated with these probably exposed the Bassian Plain several times during the epoch. Local evidence exists for only the sea-level depression during the Late Wisconsin glaciation (Gill, 1971). This most recent glacial phase greatly modified Tasmanian climates between 40 000 and 10 000 y BP (Bowler et al., 1976) and the coincident worldwide drop of sea-level of over 130 m (Milliman and Emery, 1968) caused the latest connection of Tasmania and the mainland. Rawlinson (1974) took rates of sea-level change from several sources. His findings allow the determination of postglacial isolation dates of various land masses relevant to the discussion below, from depths shown on navigational charts; these dates appear in Table 4.1. Bass Strait was last dry from 22 500 until 12 750 y BP; during this whole time, southern Australia was undergoing full glacial climatic conditions (Rawlinson, 1974). Figure 4.5 shows the coastline of south-east Australia at 18 000 y BP, assuming that the sea was 150 m below its present level. The outline and extent of glacial-periglacial and alpine-subalpine zones are taken from a map presented by Rawlinson (1975).

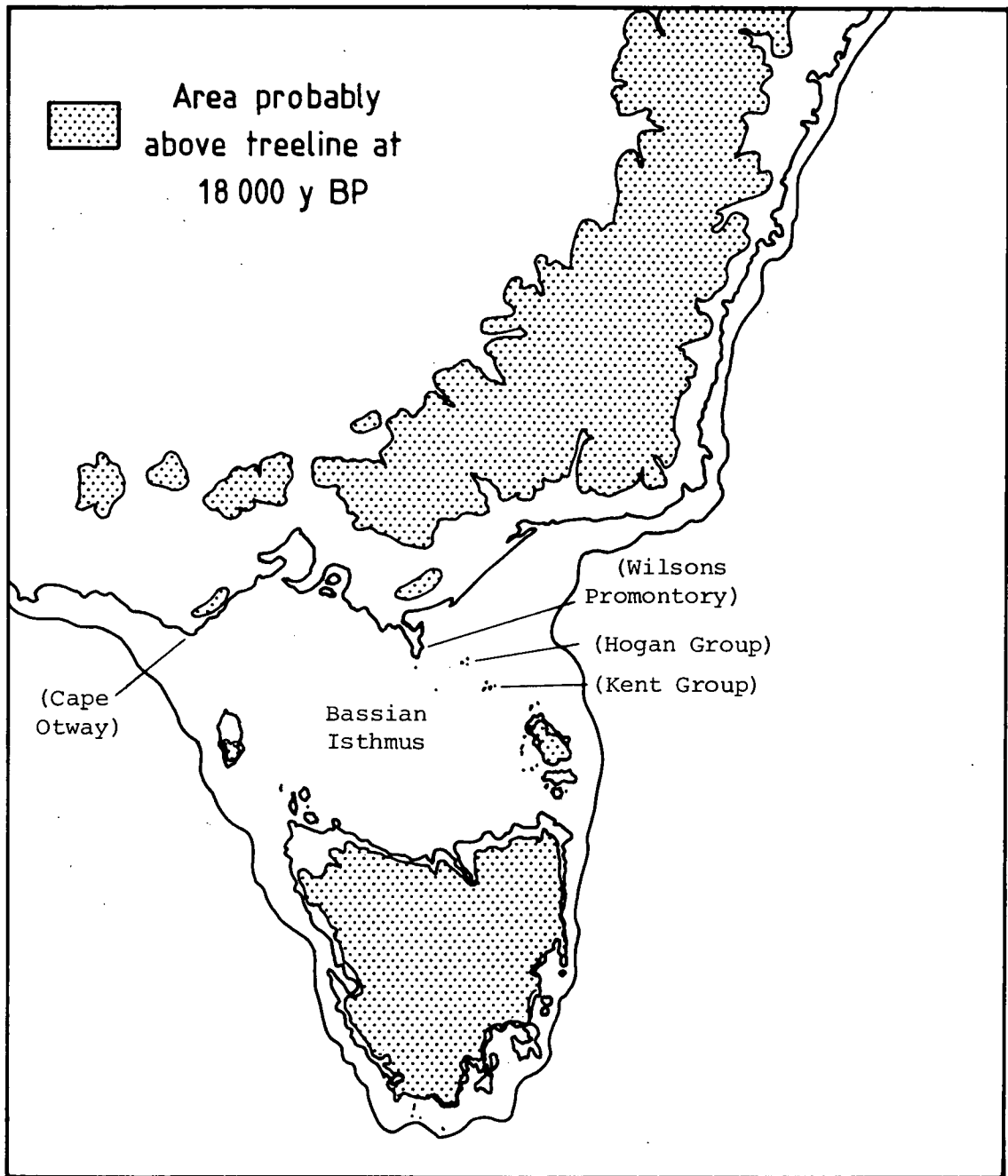


Figure 4.5 Reconstruction of south-east Australian environments at about 18 000 y BP, showing areas of glacial-periglacial and alpine-subalpine influence (above treeline). Supposed coastline corresponds to -150 m contour of present day. Present coastline superimposed for reference, modern place-names bracketed. Adapted from Rawlinson (1975).

These zones correspond approximately to the area which was above the timberline in Tasmania before 11 500 y BP, according to Macphail (1979). Low-lying tracts of land bore sclerophyll forest, herbfield or grassland according to the amount of precipitation at each locality.

Previous environments in Tasmania: late Mesozoic to Recent

Cretaceous

During the Cretaceous period, the Australian continent (including Tasmania) was still part of the Gondwana landmass. Tasmania was at a much higher latitude than its present position (Crook and Belbin, 1978). Global climatic patterns differed greatly from those experienced today, however; Cretaceous laterite and bauxite found in northern Tasmania give evidence of a hot, humid climate (Banks, 1973). The Gondwana supercontinent supported mixed forests of austral gymnosperms and evergreen angiosperms (Raven and Axelrod, 1972) and it seems that suitable habitats for landhoppers (see Section 4.4) were widespread.

Tertiary

A review of the paleoclimatic and paleobotanical data relevant to Australia during the Tertiary has been presented by Kemp (1978). The sequence suggested by her is outlined below, with some evidence from other sources.

During the Paleocene, seas in high latitudes were considerably warmer than they are today, partly because the arrangement of the continents allowed equatorial currents to travel long distances unimpeded by land (Frakes and Kemp, 1972). Greater uptake of heat and its subsequent distribution north and south contributed to widespread tropical climates, as high ocean temperatures caused high evaporation and precipitation. There is no evidence for an Antarctic ice-cap at this time. A zone of westerlies influenced much of southern Australia, where rain-bearing winds penetrated deep inland. Rainforest vegetation dominated the Australian landscape

at this time, and continued to do so until the Miocene. Australia separated from Antarctica in the middle of the Paleocene, at about 55 My BP (Wessell and Hayes, cited by Crook and Belbin, 1978), but the Tasman Rise (south of Tasmania) prevented circumpolar currents. Gentle temperature gradients between equator and pole therefore persisted.

Hos (1975) found palynological evidence of closed canopy rainforest in south-west Western Australia during the late Eocene. During this epoch, the species richness of pollen at this and other southern Australian sites decreased, with the loss of species indicative of warmer climates. Oxygen isotope measurements reveal progressively lower ocean temperatures over this time.

The Eocene-Oligocene boundary (about 40 My BP) was marked by a distinct drop of temperature in Victoria (Dorman, 1966) and other southern hemisphere localities (Frakes, 1978). Circumpolar currents developed around Antarctica as the ocean deepened between that continent and Australia. Significant build-up of ice on Antarctica probably began about this time, although glaciers did not reach the sea until about 26 My BP. Temperature gradients between the equator and the pole steepened. The Australian flora of this time is not well known, but apparently displayed floristic similarities with today's cool temperate forests.

Miocene climates in Australia were influenced by the northward drift of the continent and the growth of the Antarctic ice-cap to near its present extent. While the southern half of Australia was influenced by westerlies, northern and north-western zones became increasingly arid as evaporation over the cooling oceans lessened, and these areas moved northwards into drier climatic belts (Raven and Axelrod, 1972; Beard, 1977). Zonation of the vegetation was marked for the first time, with grasslands in the centre and rainforest persisting in eastern and southern areas where year-round rains apparently prevailed. Isolation of the western floras from those of the east occurred at some time after the Eocene, possibly as late as the upper Miocene, when circulation patterns like those

of today developed.

The Tertiary thus involved a long-term climatic change in Australia, from widespread warm, tropical conditions to cooler climates with aridity developing in the centre of the continent. Forests suitable for landhopper habitats probably occurred across the continent at the beginning of this period, contracting southwards until they reached the present-day distribution in the south-west, the south-east, and in Tasmania. The disjunct nature of these southern forests, therefore, is probably a fairly recent phenomenon.

Pleistocene

During the Pleistocene, climates were at times more severe even than those of the late Tertiary. Most available information covers the late Pleistocene-Holocene, an interval particularly relevant to the present discussion.

There is some evidence for glaciations older than the last one, found in northern Tasmania; this consists of an unconsolidated till probably older than 120 000 y BP, and an even earlier tillite. Cool, dry conditions in southern Australia prevailed before 40 000 y BP; over the next 10 000 y, precipitation effectiveness increased (Bowler *et al.*, 1976). This was possibly due to a drop in temperatures at the beginning of the most recent cold phase. Between 30 000 and 25 000 y BP, glaciers were active in Tasmania, periglacial activity occurring at low altitudes. During the next 10 000 y, the lowest temperatures on the Australian mainland were experienced (Bowler *et al.*, 1976), and the sea levels dropped as water was locked up in ice, reaching their minimum at 20 000 - 18 000 y BP (Gill, 1971). During this time, the greatest aridity on the Australian mainland occurred (Bowler *et al.*, 1976).

Pollen studies in Tasmania give some indication of the local vegetation during the last glaciation. Between 28 000 and 14 700 years ago, the area north of Tasmania, exposed by low sea levels, supported open

shrubland and later, grassland, becoming more open, with abundant composites. Eucalypts were present in the area, but sparse. This cold steppe formation probably extended from the Adelaide region in South Australia down to and across the Bassian Plain, subjected to colder, drier and possibly windier conditions than occur today (Hope, 1978). At the closing stages of glaciation, Tasmania probably also bore sparse grasslands in lowland situations. Climates there too were cold and dry, and a west-east precipitation gradient existed, causing "glacial-arid" conditions in eastern Tasmania (Macphail, 1975, 1979). Any forests which existed probably consisted mainly of eucalypts and *Acacia*, and occurred on the continental shelf. Rainforest species survived as minor constituents of scrub in western Tasmania, on lowlands or occupying wet gullies. The climatic timberline was near present-day sea-level in the west and at about 400 m in the east.

The reforestation of Tasmania during the period of postglacial rising temperatures has been intensively studied by Macphail (1975, 1976, 1979; Macphail and Peterson, 1975; Macphail and Jackson, 1978). Temperatures rose rapidly from before 11 500 until 9500 y BP; precipitation levels increased and deglaciation of highland areas occurred during this period. Grasslands and heathlands were replaced by forest, although this process was retarded in the east by low rainfall. Subsequent climatic changes have been slight. Temperature and effective precipitation increased somewhat to a climatic optimum occurring between 8000 and 5000 y BP. Similar climatic optimum conditions have been recorded in Chile, at 8500 - 6500 y BP (Heusser, 1974) and in New Zealand at about 8500 y BP (Lintott and Burrows, 1973), possibly occurring later than a temperature peak in Antarctica between 11 000 and 8000 y BP (Lorius et al., 1979).

Nothofagus forest was most widespread at about 7800 y BP. Closed forests developed first, but at 4600 y BP, more open forests prevailed. Sclerophyll taxa (eucalypts) became more widespread, and the

effect of fire (largely due to man) caused rainforests to become more restricted, and *Gymnoschoenus* sedgelands to spread in the west.

Since 8000 y BP, Hunter I., off north-west Tasmania, has carried coastal shrubland like that now found there (Hope, 1978).

It is obvious then, that during the last glaciation in Tasmania, and probably in mainland Australia, landhopper habitats were severely restricted. Forest cover was apparently very limited, in great contrast to conditions which had prevailed for most of the Cenozoic, and to those found today. Even when Bass Strait was not a marine barrier, it appears that vegetation types there were not those which might be expected to support amphipod populations. The overall dryness which limited the extent of forest would not have encouraged the movement and spread of this fauna.

Section 4.3 Distribution of Tasmanian land amphipods

The information presented in this section results from collection and identification of specimens from over 500 localities in Tasmania. Data regarding the collection of this material may be found in Appendix I. The number of specimens belonging to each species is listed under "Material examined" (Chapter 3). As mentioned earlier, only species found on the mainland of Tasmania were treated; however, where these species were found elsewhere, that occurrence is recorded here.

Each map (Figures 4.6 - 4.20) represents the distribution of a species treated in Chapter 3, from the localities of material at hand. Where these localities occur very close together, however, some have not been marked. The number of collections in which each species was found is shown in the bottom left-hand corner of each map. Apparent disjunctions in distributions are marked D in Figures 4.6 - 4.20 where the species concerned is absent from a large number of samples collected between two areas of known occurrence.

Orchestiella neambulans (Figure 4.6)

This species is fairly common in western Tasmania; it is not found in areas with less than 1800 mm annual rainfall. It does not occur in the southern most part of Tasmania, on offshore islands or near the coast. It is common in inland teatree swamps.

Orchestiella quasimodo (Figure 4.7)

A somewhat similar, but more southerly distribution than that of *O. neambulans* is displayed by this species, which also shows an affinity for teatree swamp. This species rarely occurs very near the sea; the only island occurrence is on De Witt I., the largest of the Maatsuyker Group, where *O. quasimodo* was found well inland in wet sclerophyll forest. Distributions of the two *Orchestiella* species overlap between the Tyndall Range and the Olga River valley (Figures 4.6 and 4.7)

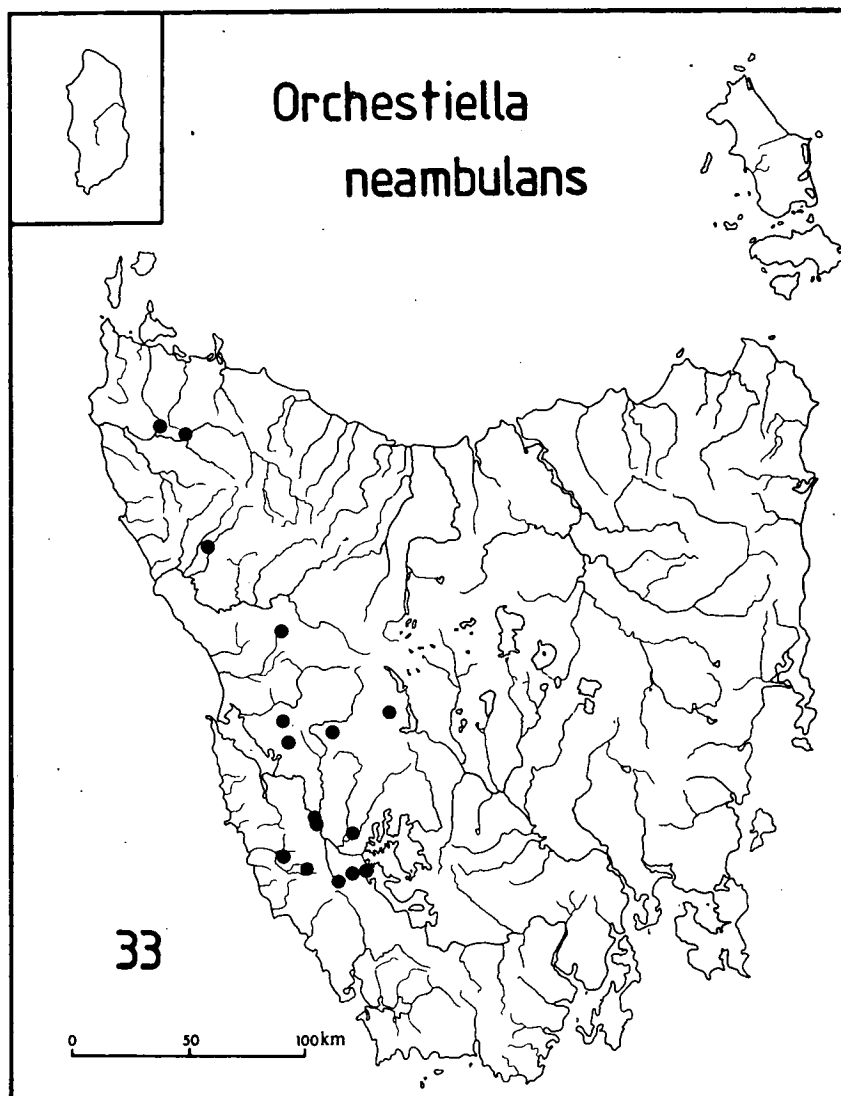


Figure 4.6 Distribution of *Orchestiella neambulans*. Total number of records is shown at lower left.

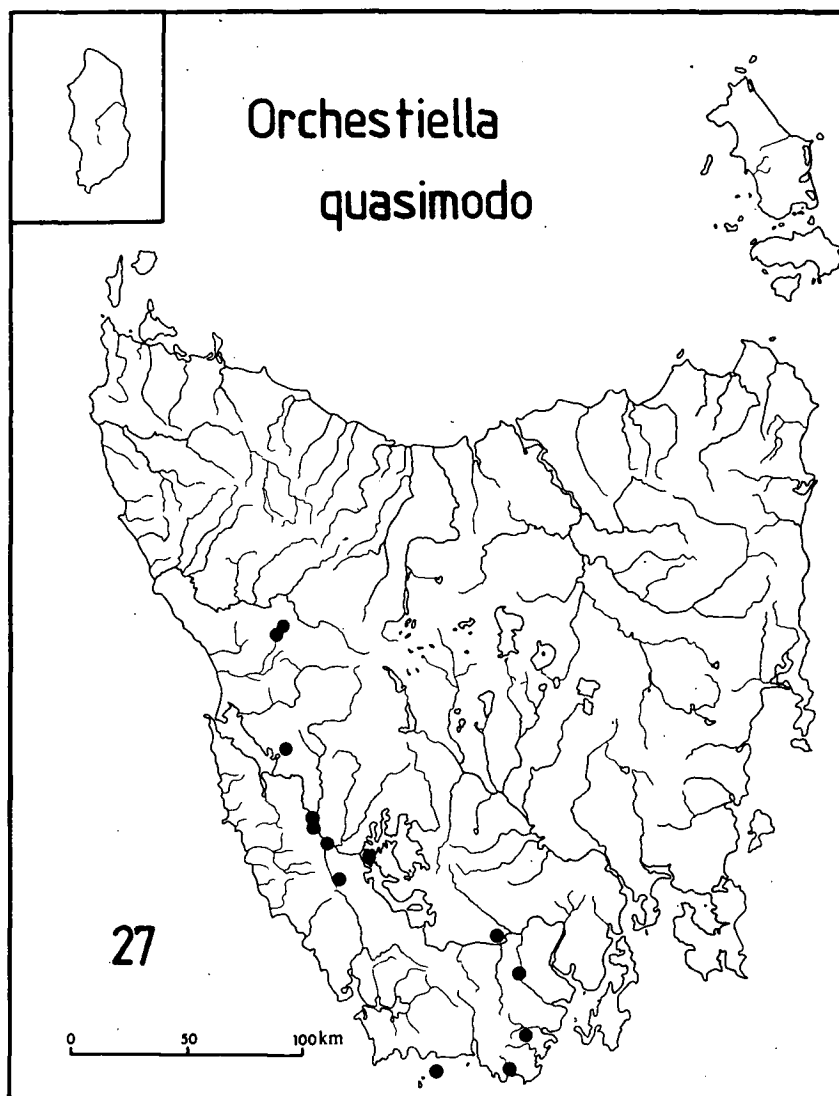


Figure 4.7 Distribution of *Orchestiella quasimodo*. Total number of records is shown at lower left.

Tasmanorchestia annulata (Figure 4.8)

This species exhibits a distribution complementary to that of the *Orchestiella* species. It is generally found in more coastal situations, except in the far north-west, where it tends to inhabit rainforest and teatree swamps as well. This last vegetation type represents a large proportion of the wooded areas in that part of Tasmania and on the nearby islands. The centre of distribution of *T. annulata* appears to be in the north-west and the Hunter Group, with coastal extensions southward. It is not found in Victoria; its King I. occurrence seems to be a northward range extension.

Neorchestia plicibrancha (Figure 4.9)

The occurrence of this species is more frequent in the southern half of western Tasmania, becoming less frequent towards the north-west. It is not found right on the coast, but occurs on De Witt I. The habitat of *N. plicibrancha* is apparently limited to wet forests, although it has been found on *Gymnoschoenus* sedgeland plains.

Austrotroides longicornis (Figure 4.10)

A relatively rare species, *A. longicornis* is mainly found in the far south, but two isolated records indicate a disjunct distribution. One of these is near Lake Rhona, in the western half of the island, and the other is on Forestier Peninsula on the east coast.

Austrotroides leptomerus (Figure 4.11)

This is another rarely-found species from the southern half of western Tasmania. It may exist in low numbers, thus turning up rarely in samples, or it may be restricted to poorly-sampled microhabitats. Both this species and the previous one occur only in rather inaccessible parts of the island, a factor which hampered more intensive searches for them.

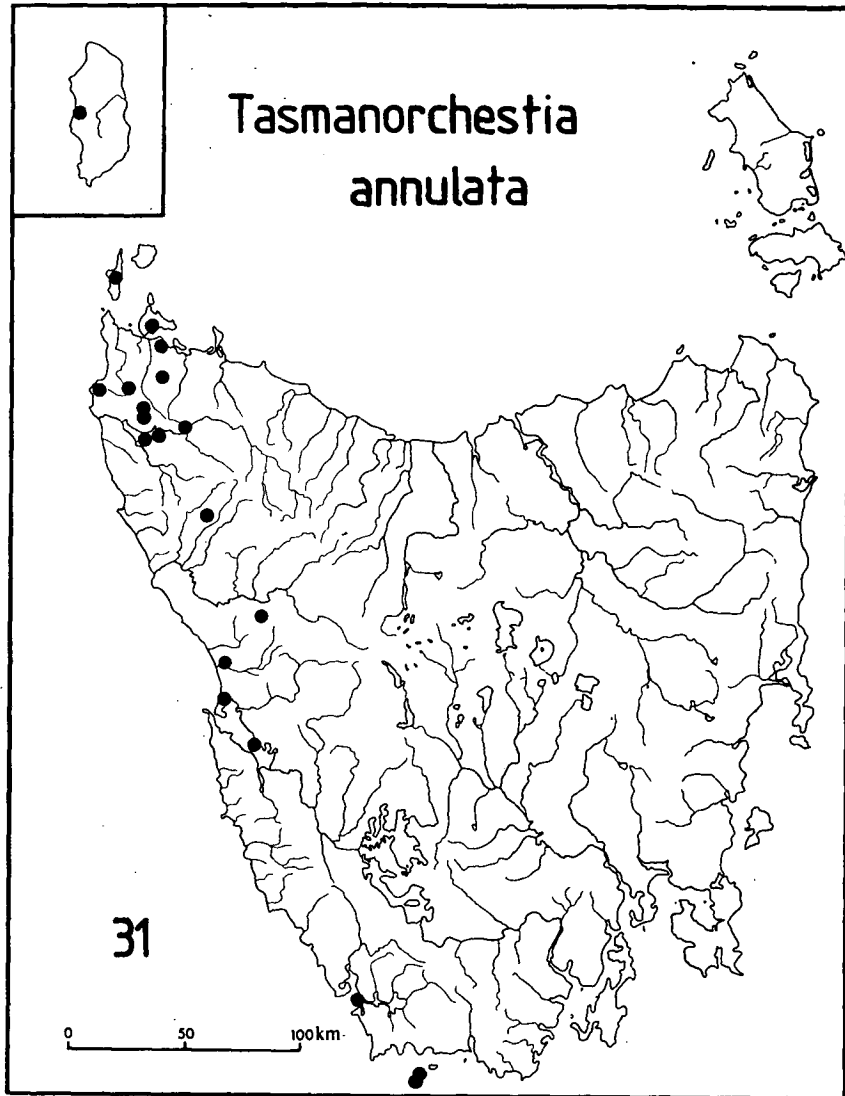


Figure 4.8 Distribution of *Tasmanorchestia annulata*. Total number of records is shown at lower left.

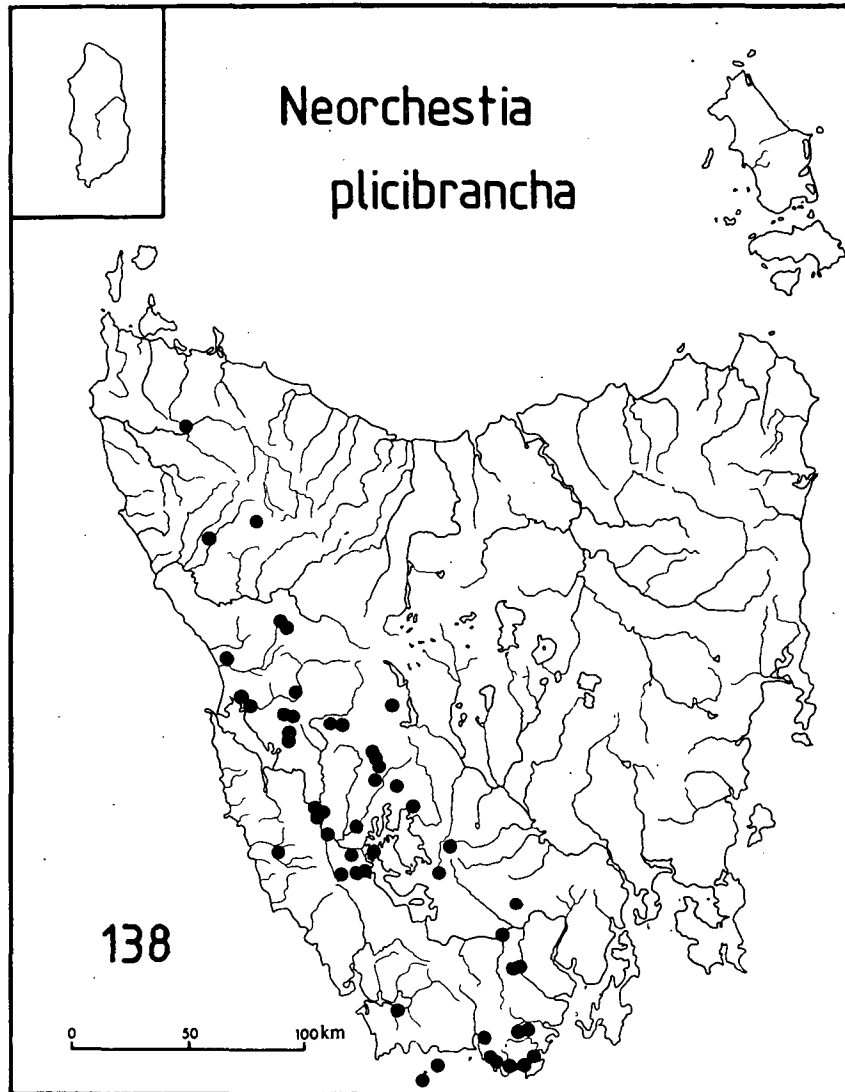


Figure 4.9 Distribution of *Neorchestia plicibrancha*. Total number of records is shown at lower left.

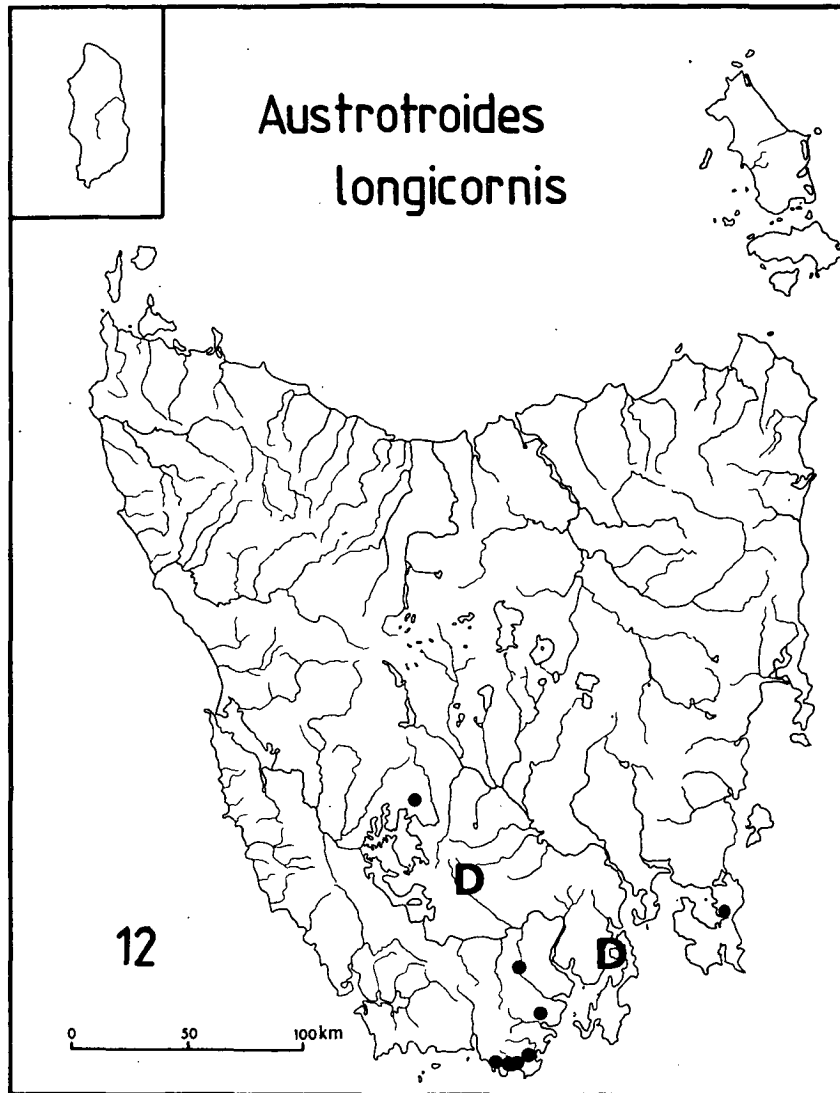


Figure 4.10 Distribution of *Austrotroides longicornis*. "D" refers to an apparent disjunction in distribution. Total number of records is shown at lower left.

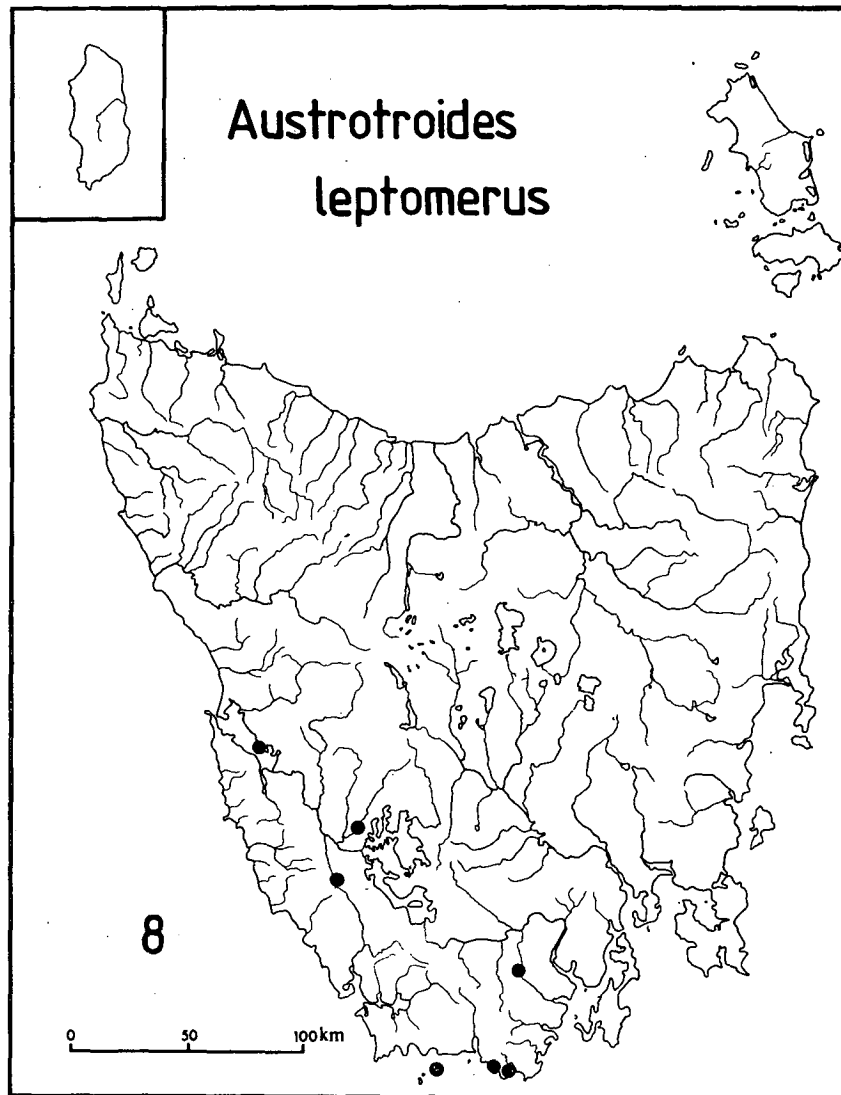


Figure 4.11 Distribution of *Austrotroides leptomerus*. Total number of records is shown at lower left.

Austrotroides maritimus (Figure 4.12)

This species is found extremely close to the supralittoral zone on the mainland of Tasmania from the west coast near Macquarie Harbour to the eastern side of the south coast. It also occurs on Tasman Peninsula; even if it is subsequently found on Bruny I., a disjunction on the mainland coast between Recherche Bay (near the south-west tip of Tasmania) to the Tasman Peninsula is indicated (D in Figure 4.12).

Mysticotalitrus tasmaniae (Figure 4.13)

While this species is most strongly distributed in the south-east and on islands off the east coast, there are a number of records in central Tasmania and on the borders of the western high-rainfall areas.

Mysticotalitrus crypticus (Figure 4.14)

This species is also centred in the south-east, but is more strongly represented in the west and south than *M. tasmaniae*. It is also found on Maatsuyker and De Witt Is., off the south coast.

Arcitalitrus sp.S. (Figure 4.15)

Having a mainly Victorian distribution, this is the only mainland Australian species occurring in Tasmania today. It displays a strong presence on King, Hunter and Robbins Is., but has been found on the Tasmanian mainland at only one locality, in teatree swamp in the far north-west.

Keratroides albus (Figure 4.16)

This burrowing species is mainly distributed in inland forests and woodlands of the western high-rainfall area, but does not occur in the far south or in the extreme north-west. It is not found in many coastal situations.

Keratroides vulgaris (Figure 4.17)

If this proves to be a single species (Section 3.3) it has the most ubiquitous occurrence, being found in litter all over Tasmania. It also

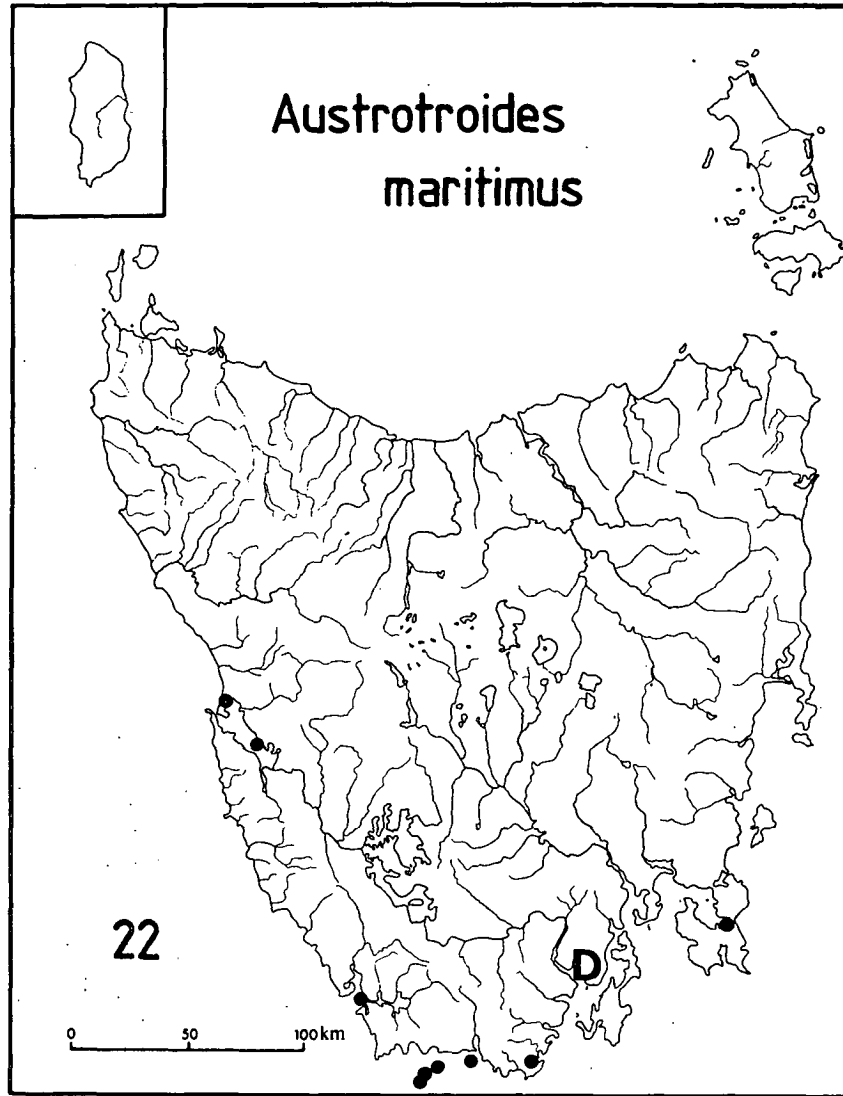


Figure 4.12 Distribution of *Austrotroides maritimus*. "D" refers to an apparent disjunction in distribution. Total number of records is shown at lower left.

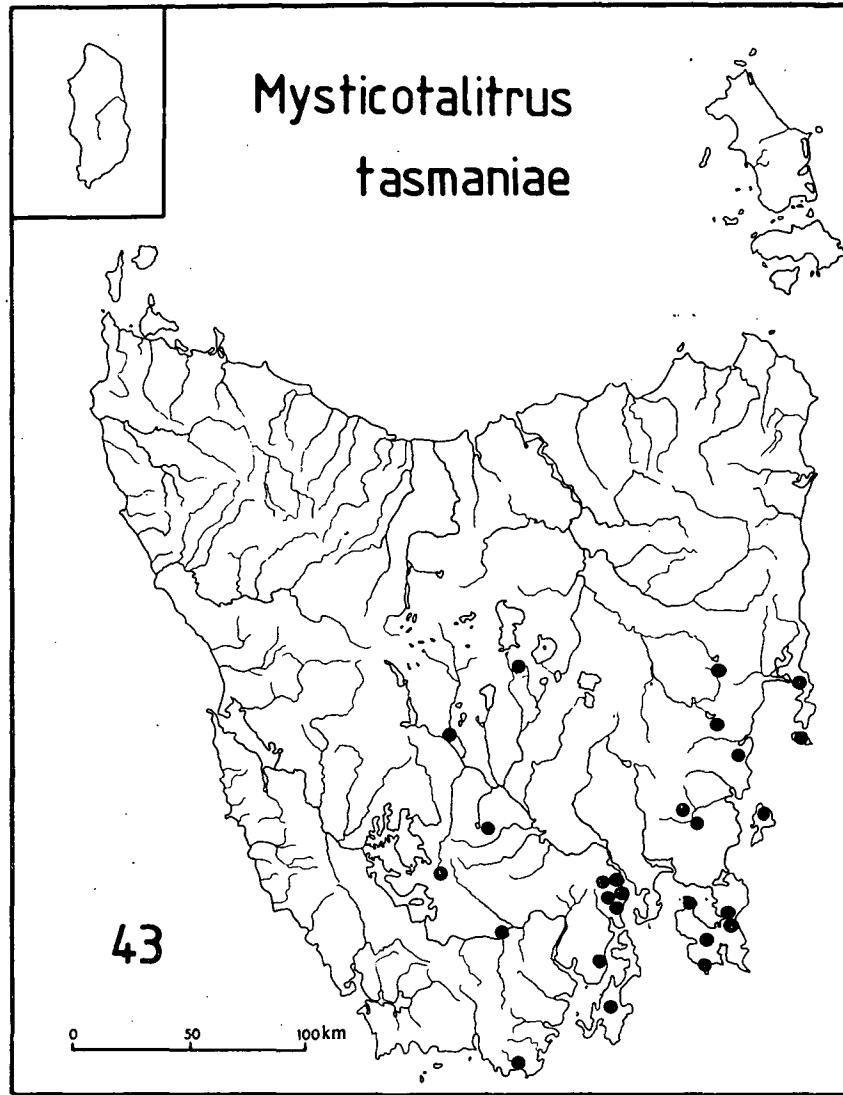


Figure 4.13 Distribution of *Mysticotalitrus tasmaniae*. Total number of records is shown at lower left.

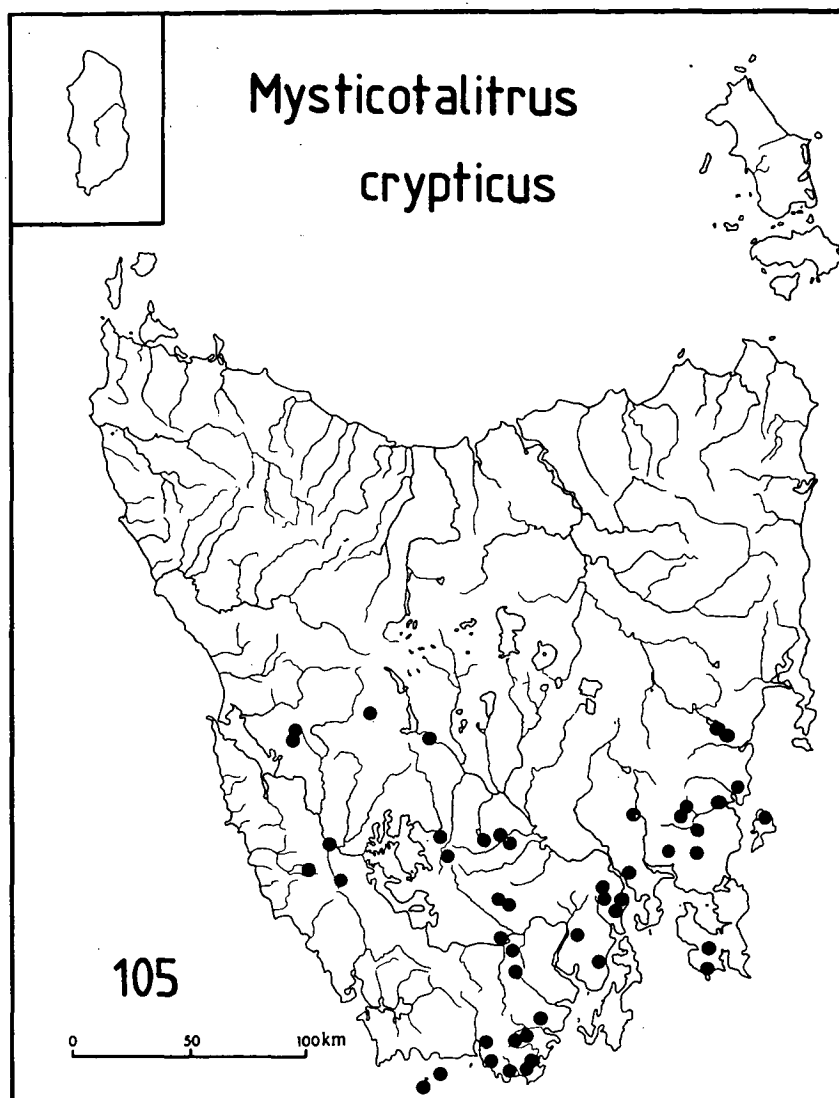


Figure 4.14 Distribution of *Mysticotalitrus crypticus*. Total number of records is shown at lower left.

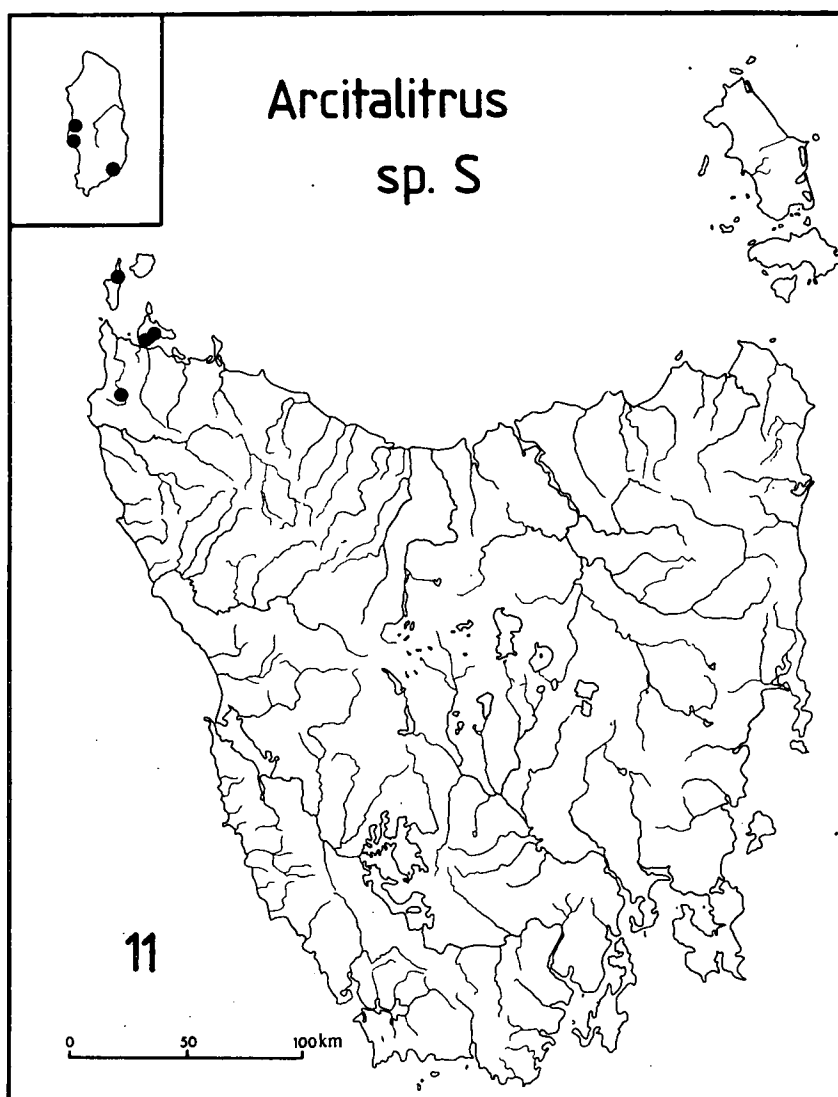


Figure 4.15 Tasmanian distribution of *Arcitalitrus* sp.S. This species is also found in Victoria. Total number of Tasmanian records is shown at lower left.

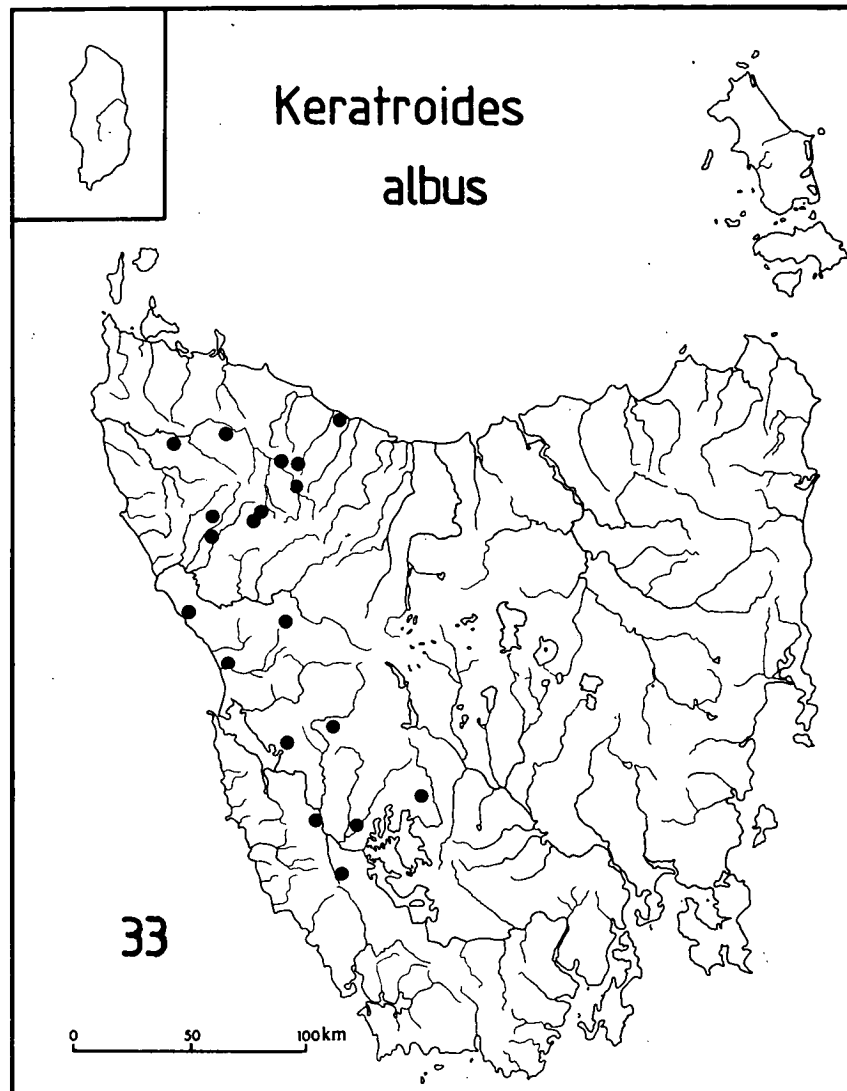


Figure 4.16 Distribution of *Keratroides albus*. Total number of records is shown at lower left.

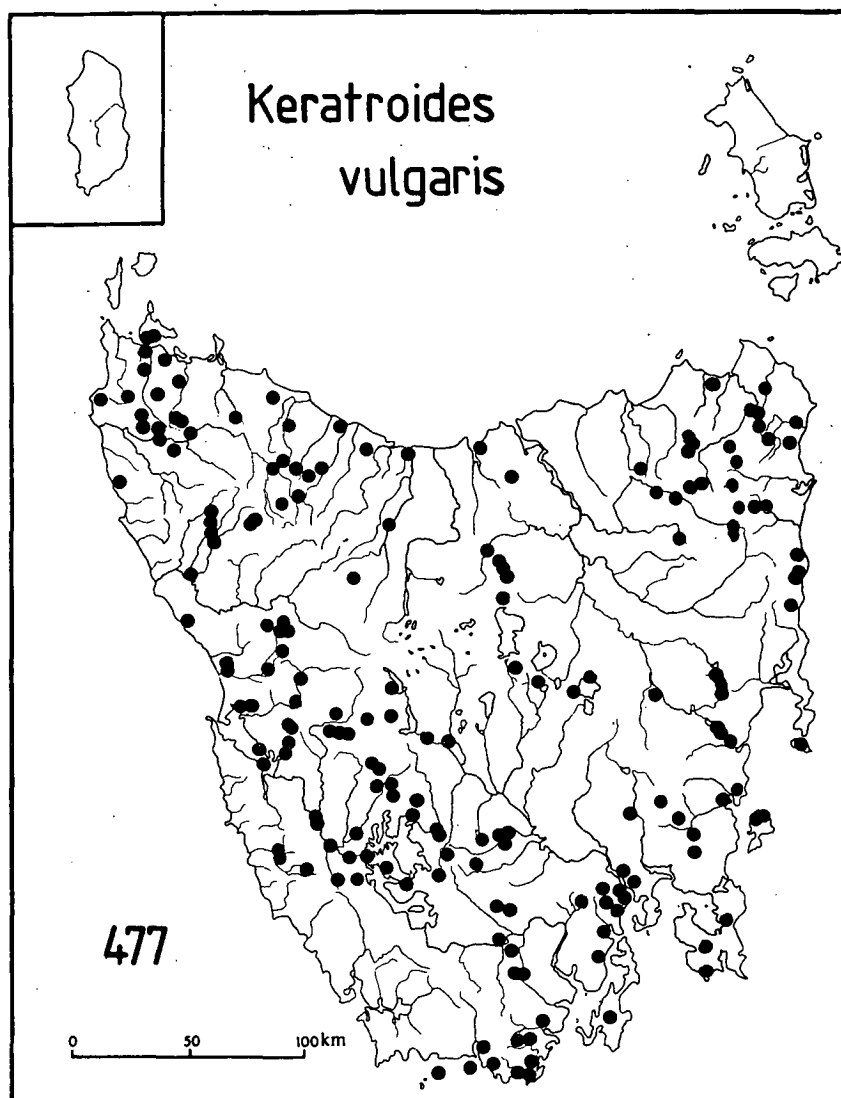


Figure 4.17 Distribution of *Keratroides vulgaris*. Total number of records is shown at lower left.

occurs on Schouten, Maria and Bruny Is. off the south coast (not on Flat Witch or Maatsuyker Is.) and on Robbins I. (not on Hunter or King Is.) to the north-west. Significantly, it has not been found on Swan I., which is a small island just off the north-east tip of the Tasmanian mainland (see below, this section).

Keratroides rex (Figure 4.18)

This species is restricted to coastal situations around the north and west coasts, and on all sampled islands off those coasts, including the Maatsuyker and Hunter Groups and King I. It only occurs very close to the supralittoral zone, except on small islands.

Keratroides pyrensis (Figure 4.19)

This species occurs in a small area in north-eastern Tasmania, and also possibly on Flinders I.

Keratroides angulosus (Figure 4.20)

K. angulosus occurs in forested areas, near but rarely beside the sea along the north, east and south coasts. This distribution is apparently continuous, in a broad curve between the northern west coast and the east coast near Maria I., but there is a major disjunction between this and another set of records on the south coast (D in Figure 4.20). This southern presence includes several records on De Witt and Maatsuyker Is.

Present patterns of species distributions

The land amphipods of Tasmania show a range of distribution patterns, but these may be broadly classified into three groups, the western forest group, the eastern forest group and the coastal group.

a) The western forest group

Orchestiella neambulans

O. quasimodo

Neorchestia plicibrancha

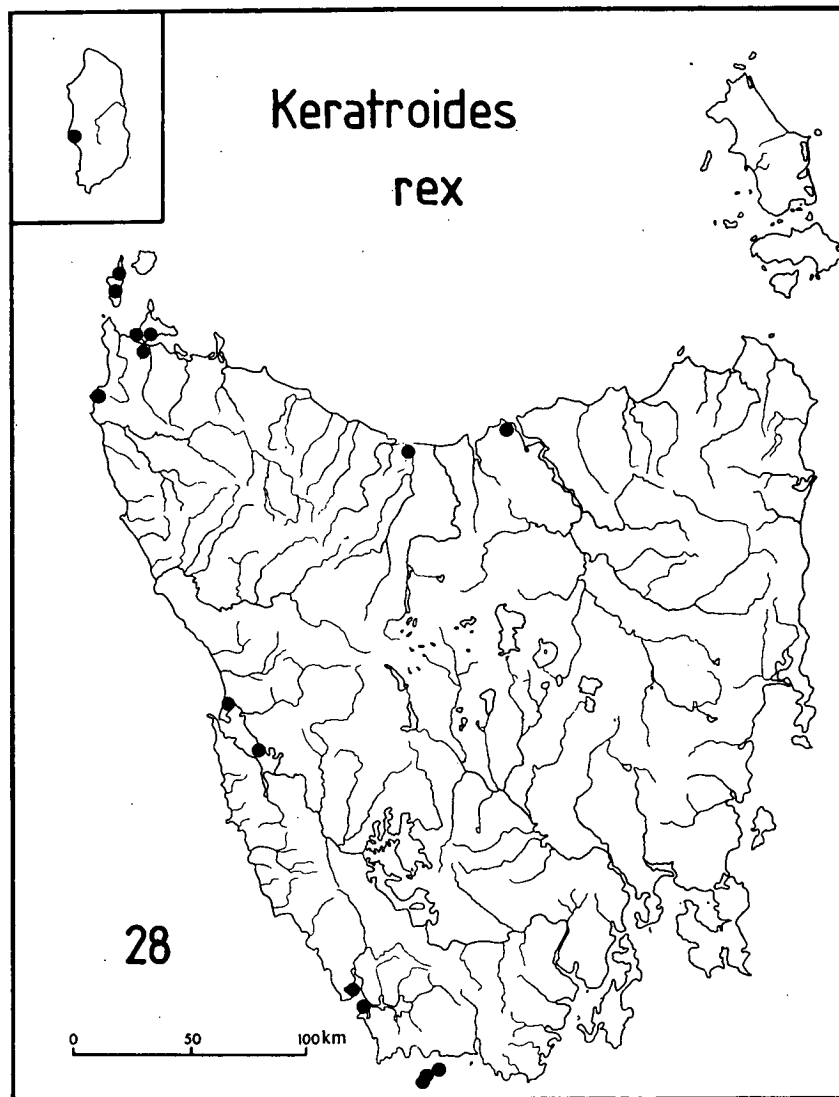


Figure 4.18 Distribution of *Keratroides rex*. Total number of records is shown at lower left.

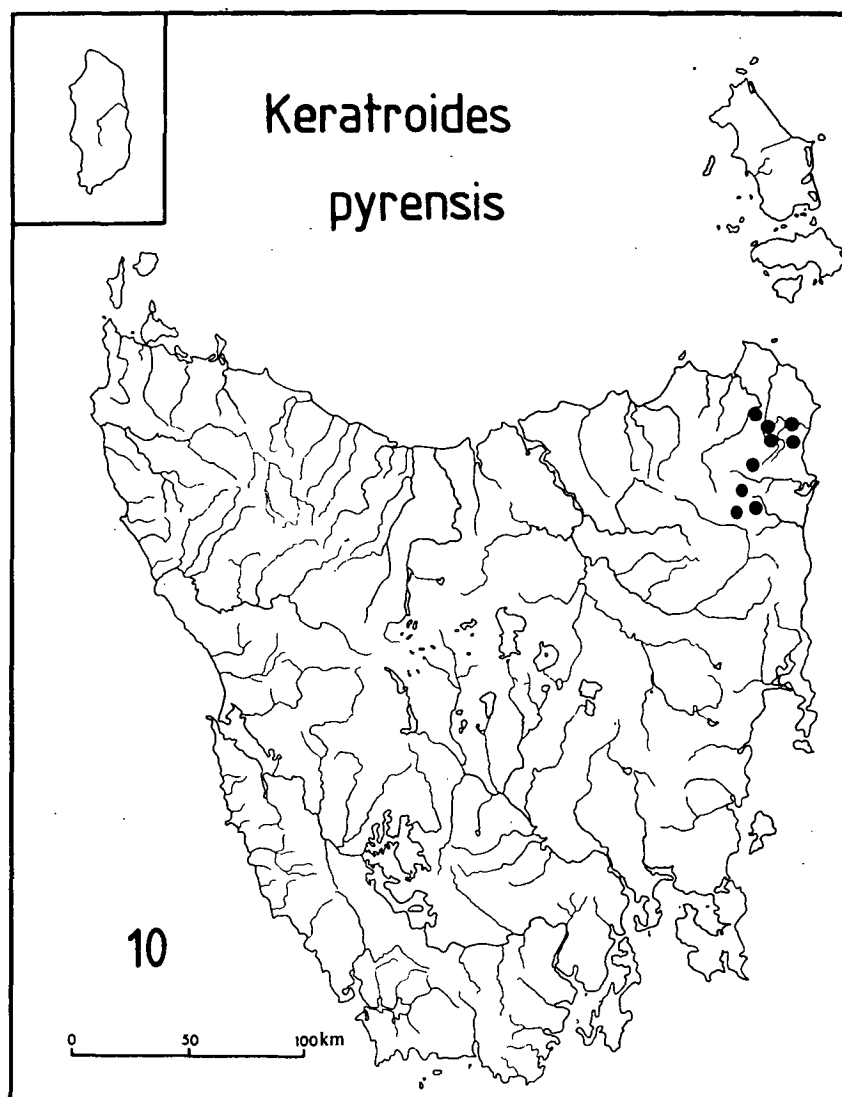


Figure 4.19 Distribution of *Keratroides pyrensis*. Total number of records is shown at lower left.

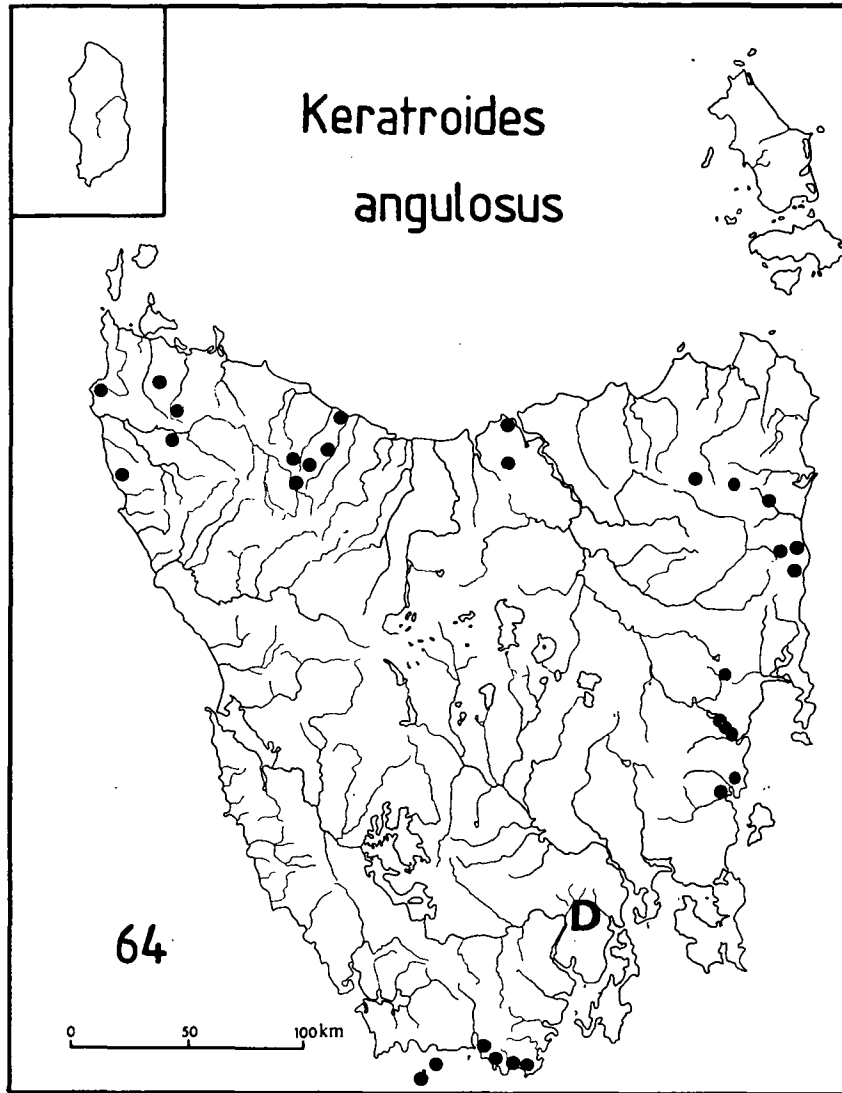


Figure 4.20 Distribution of *Keratroides angulosus*. "D" refers to an apparent disjunction in distribution. Total number of records is shown at lower left.

*Austrotroides longicornis**A. leptomerus**Keratroides albus*

This group includes species which are restricted to the western half of the island, and are almost exclusively found in forest habitats. As shown in Figure 4.2, this area experiences the highest rainfall in Tasmania, while the most important forest communities are rainforest and wet sclerophyll forest. It is interesting to note that none of the landhopper species of this group are found in the substantial high-rainfall area in north-east Tasmania around the Ben Lomond massif and the mountains to the north. Precipitation in this region is not as high as in some parts of the west, but it is high enough to allow the development of climax *Nothofagus* rainforest. The absence of the western amphipod group implies that this tract of rainforest has always been disjunct from those of western Tasmania. In fact, Macphail's findings (1975, 1979) suggest that the occurrence of rainforest here is of postglacial origin. The glaciation of the area in the Late Wisconsin was very limited (Derbyshire, 1972) despite its altitude (up to 1573 m). This was apparently due to low precipitation levels prevailing in eastern Tasmania during the last glaciation. It is probable, therefore, that the western forest group survived this glacial period in lowland forest remnants in the west and has not colonized the eastern rainforest since then.

b) The eastern forest group

*Mysticotalitrus tasmaniae**M. crypticus**Keratroides vulgaris**K. pyrensis**K. angulosus*

While these species occur in forests in the drier eastern side of Tasmania, all but *K. pyrensis* are also found in the west. On the other

hand, each of these species shows a different distribution pattern, and these will be discussed individually elsewhere.

c) The coastal group

Tasmanorchestia annulata

Austrotroides maritimus

Keratroides rex

These species are restricted to coastal situations to various degrees. *A. maritimus* and *K. rex* occur only within a few metres of the shore. One might speculate that these species are restricted to this habitat by a poorer ability to retain ions than is possessed by the forest species, as suggested by MacIntyre (1954) in the case of the sandhopper *Talorchestia quoyana* (Milne Edwards).

Tasmanorchestia annulata is found further inland than the other two species, but is also found with them, and the three species together form the landhopper fauna typical of small western and southern islands around Tasmania. *T. annulata* is a common forest species only in the far north-west, where the species of the western forest group are poorly represented or absent. In the south, this species may therefore be restricted by competition to the coastal areas.

Distribution of genera

While the ecological groupings above are a useful way to describe modern distributions, the history of the terrestrial amphipod fauna may be better elucidated by comparing the distributions of related species. This is done within generic units.

The endemic genera

Orchestiella and *Tasmanorchestia* are found only in Tasmania, although relationships with *Agilestia*, from Victoria and Queensland, may be established. The component species of these genera are all found in western Tasmania, with *T. annulata* occurring on southern, western and

north-eastern offshore islands and King I. This northern range extension is apparently only recent, as there is no apparent morphological divergence between specimens from isolated populations.

Mysticotalitrus is also endemic to the Tasmanian area, with the distribution of both species centred in the south-east of the Tasmanian mainland. Both occur on islands off the east coast, the range of *M. crypticus* including De Witt and Maatsuyker Is. and extending further into the west than that of *M. tasmaniae*. It is likely that both species were restricted to southern relict forest areas during the height of the recent glacial-arid period, extending northward during deglaciation to colonise the east coast islands before they were isolated. On the other hand, morphological differences between populations of *M. tasmaniae* north and south of the Derwent River (Section 3.3) point to a possible disjunction at some time, and gene flow within that species may still be restricted.

Both species of *Mysticotalitrus* are able to live in much drier situations than those usually found in the western half of the island. Unlike *Keratroides vulgaris* however, these species are not strongly represented in the wetter areas.

Mysticotalitrus may be related to the *Talitriator eastwoodae* Methuen complex of South Africa (E. L. Bousfield, pers. comm.). If this is so, and the modern distributions are due to continental drift, an origin of the group before the end of the Cretaceous is implied (McKenna, 1973).

Neorchestia

Another species of *Neorchestia* occurs in the south-western wet sclerophyll forests of Western Australia. This disjunct distribution is presumably the result of a former wide occurrence of this genus. Southern Australia has experienced long periods of mesic climate (Section 4.1) and Tasmania has been linked to the mainland during some of this time. On the basis of the present-day distribution of *Eucalyptus diversifolia*

and *E. incrassata*, Parsons (1969) has argued that Late Pleistocene low sea levels led to forested coastal areas south of the Nullarbor Plain, which could have provided migratory routes for forest taxa. However, the morphological divergence between the species of *Neorchestia*, as well as that between the species of *Austrotroides* from the two areas (see below), is consistent with the continuous distribution of these genera across southern Australia much earlier than the late Pleistocene. In addition, evidence produced by Hope (1978) suggests the existence of an extensive grassy plain between Adelaide and north-west Tasmania at that time. It is likely, therefore, that any forest development on the southern coastal plains was an open, dry sclerophyll forest or savannah woodland formation typical of low precipitation levels (Macphail and Jackson, 1978). This would provide no suitable habitat for the fauna of mesic forests, especially amphipods.

Austrotroides

The Tasmanian species of *Austrotroides* show sometimes disjunct distributions confined to the south of the island. While generally restricted to wet forests, *A. longicornis* and *A. leptomerus* are often found in drier microhabitats than sympatric species, while *A. maritimus* is strongly confined (on the Tasmanian mainland) to backshore habitats. These disjunct distributions (Figures 4.10 and 4.12) provide evidence of restriction of previously wider distributions. This can be understood in terms of the late Pleistocene contraction of forest habitats; it is possible also that the two forest species have not since returned to their former ranges because of competition with more advanced forms like *Keratroides vulgaris* (see below).

The existence in Western Australia and South Australia of further *Austrotroides* species (Friend in MS: see Appendix) implies that ancestors of these species inhabited the extensive southern forests of the Cretaceous and Tertiary periods at some time. The Tasmanian and

mainland Australian groups can be distinguished from each other today, so it appears that the groups were derived from different, though related, progenitors. The distinctness of the western and South Australian forms from each other also casts doubt on the availability of a late Pleistocene migration route south of the Nullarbor, at least for amphipods.

Both groups of *Austrotroides* display a number of apomorphic features, such as the large anseriform posterior gills and reduced pleopods. It is thus certain that the progenitors of these groups, and their common ancestor, also possessed these features, which are evidence of substantial adaptation to the terrestrial environment. Two of the present-day mainland Australian species (*A. occidentalis* and *A. crenatus*) are found in drier habitats than most land amphipods. It is interesting to consider, therefore, whether the ancestral *Austrotroides* occurred in dry or wet habitats. Two possibilities are as follows:

- 1) The predecessor of *Austrotroides* was adapted to dry forests, but the Tasmanian colonist moved into moister southern forests and radiated into those habitats. In support of this alternative are the morphological adaptations to life on land, which might have occurred more quickly in dry habitat. Modern Tasmanian species appear to inhabit dry microhabitats within the wet forest ecosystem.

- 2) The ancestor of *Austrotroides* was adapted to wet forests. Tasmanian species arose and persist within this habitat (except *A. maritimus*, which lives in wet coastal habitats). The Australian species also appeared in wet forests but with the development of aridity during the Tertiary (Beard, 1977) were pushed to south-coastal ranges and trapped in habitats which became progressively drier. In support of this alternative is the fact that one Western Australian species (*A. pectinalis*) is found in fairly wet forests, placing the dry-forest-adapted species in a 2-4 minority.

The second alternative appears more reasonable, because Tertiary climates in southern Australia were generally mesic (Section 4.1).

The relationship between the amphipod faunas of Tasmania and Western Australia is by no means unique. Spencer (1898), in delimiting Australian faunal provinces, united Tasmania and south-west Western Australia with parts of Victoria and coastal New South Wales in the Bassian province. He separated this from the arid Eyrean and tropical-subtropical Torresian provinces.

Arcitalitrus

This is a morphologically apomorphic genus, possibly in a phase of expansion. *Arcitalitrus sylvaticus* is an opportunistic species which is common in gardens of Melbourne and Sydney, although being replaced to some extent in Sydney by the introduced *Talitroides topitotum* and *T. alluaudi*. Centres of distribution of this genus appear to be near the New South Wales-Victoria border, where five species are found, and the New South Wales-Queensland border, where there are four species, the only species common to the two areas being *A. sylvaticus*. *A. sp.S.* is a Victorian species occurring in a wide range of habitats from wet to dry sclerophyll forest in Victoria, surviving in fairly open situations in coastal heath, as well as teatree woodland, in the Hunter Group.

It is most likely that this species moved into Tasmania during the last glaciation, and that this invasion occurred along the western side of the Bassian isthmus, isolating populations, which persist on those islands today. This side of the isthmus apparently bore more shrubs and patches of woodland than other exposed land in Bass Strait (Hope, 1978) because of higher rainfall from the westerlies.

While *A. sp.S.* has survived well on the islands, it appears to be ecologically restricted to the far north-west of the Tasmanian mainland, possibly through interaction with other landhopper species. The distribution of the bullfrog *Limnodynastes peroni* resembles that of *A. sp.S.* (Littlejohn and Martin, 1974) and may be influenced by similar factors.

Keratroides

Species of this genus show a variety of distribution patterns which seem to bear little relationship to each other. However, if they are examined closely, several interesting facts emerge.

The genus *Keratroides* comprises three subgroups: *Keratroides albus*, the most morphologically specialised species, the *vulgaris*-group and the *angulosus*-group. As mentioned in Chapter 3, the *vulgaris*-group is found in Tasmania and on some eastern Bass Strait islands, while the *angulosus*-group is found in Victoria, in Tasmania and also on eastern Bass Strait islands.

Although *Keratroides albus* is the species most specialised for a particular microhabitat, it is the only species of the genus with biramous setose pleopods, a plesiomorphic feature. It shows a western forest distribution and does not occur off the Tasmanian mainland. These observations suggest that the ancestor of *K. albus* was an early offshoot from the *Keratroides* line which became established in Tasmania before the arisal of the other extant species of the genus. A Tasmanian origin for the group is therefore postulated, followed by a northward spread of the genus as far as Victoria.

This hypothesis is supported by the modern distribution of the *vulgaris*-group, of which the northern-most presence is on the Hogan Group. This group reaches its greatest diversity in the Furneaux Group, where six species have been found.

The *angulosus*-group includes the most apomorphic species of the genus, and consists of at least five species. One of these occurs on the Tasmanian mainland, two on the eastern Bass Strait islands, and two or more in Victoria.

While distributions appear to have been modified by events in the last 30 000 years (see below), *Keratroides* seems to have been established in both Tasmania and Victoria before their latest land connection.

Bass Strait island faunas

The landhopper fauna of the western Bass Strait islands (Hunter Group and King I.) shares species with Tasmania and Victoria, differing completely from the fauna of the eastern islands in the Strait, which is highly endemic. This situation is unusual among animal groups, in which distinct faunal elements have tended to arise on King I., apparently due to long-term isolation. An endemic emu, *Dromaius minor* has become extinct there since white settlement (Green and McGarvie, 1971), while a distinct race of potoroo (*Potorous apicalis*), smaller and darker than Tasmanian mainland specimens, occurs there today (Green, 1974). Hynes and Hynes (1980) decided that King I. representatives of the stonefly *Reikoperla triloba* deserved subspecific recognition. An explanation of the rather different situation found amongst the landhoppers of Bass Strait follows.

The western land link

The four terrestrial amphipod species occurring on King I. are all found in either Victoria or Tasmania, suggesting that their occurrence on King I. results from the existence of continuous populations during a recent period of dry land connection, probably in the last glaciation. The two Victorian species, found there, *Arcitalitrus* sp.S. and another undescribed species (new genus), both occur in fairly dry habitats in Victoria, as well as in dry sclerophyll forest. The two Tasmanian species, *Tasmanorchestia annulata* and *Keratroides rex*, both belong to the coastal group and were in fact found in situations near the west coast of King I. The dry climate and shrubland-grassland vegetation of the isthmus during the period of connection have already been described, and consequently it is not surprising that the Tasmanian forest amphipods are not represented today on King or Hunter Is.

The eastern land link

At the most recent time of lowest sea-level, a slight ridge ran

in a north-westerly direction between Tasmania and Victoria on the eastern side of the Bassian Isthmus. Raised above the general level of this ridge were a number of granite knolls, which today are islands, such as Curtis and Rodondo and the Kent and Hogan Groups. The most striking features would have been the peaks still exposed on Flinders and Cape Barren Is.

There are very little data indicating the nature of environments on this side of the Bassian Isthmus during this period of exposure. Macphail (1975) postulated a strong west-east decrease of precipitation for Tasmania at that time, but due to the low relief of the western margin (Jennings, 1959), this rain-shadow effect on the moisture-bearing westerlies would have been much weaker across the isthmus. The eastern granite hills may have caused some local orogenic rain allowing the development of wooded pockets, but these were surrounded on all sides by extensive *Poa* grasslands which apparently covered much of the isthmus (Hope, 1978).

The landhoppers so far found on the eastern Bass Strait islands (from the Kent Group to Swan I.) belong to eight species, all of which are in the genus *Keratroides*, and all of which, with the possible exception of one species, are endemic to that island chain. This, then, is a distinctive fauna apparently adapted to a particular environment not found on either mainland. The occurrence of several of these species on a number of different islands suggests that there was movement between those areas of the isthmus and that species have not arisen since isolation. During the final stages of deglaciation (11 500 - 9500 y BP), rainfall increased markedly (Macphail, 1975) probably causing an increase in woody vegetation near these eastern hills. A range expansion by amphipods might then be expected on parts of the isthmus still exposed. By this time, however, most of the island groups were already isolated (Table 4.1) so the distribution of species on the islands was apparently due to previous movement across grassland habitats.

There is no trace of any of these species on King I. or the Hunter Group, so they appear to have been absent from this side of the isthmus.

Two alternative hypotheses are advanced in explanation:

a) The eastern group reached the western margin but could not compete with those species on that side, where rainfall was high enough to support both groups.

b) The eastern group was limited to areas on the eastern side and did not cross the central plain. The grassland (?) of the central Bassian Plain may have been a less suitable amphipod habitat than that between the eastern granite outcrops.

Both explanations are plausible on the basis of the data available. A discussion of competition which has some bearing on this matter may be found below.

Range expansion by Keratroides vulgaris

The distribution of *K. vulgaris* (Figure 4.17) stands out amongst that of other Tasmanian species because of its almost ubiquitous presence on the main island. At the same time it is noteworthy that while occupying Schouten, Maria and Bruny Is. in the east, it is present on only a few of the islands off other coasts, and then only those closest to the mainland (Ile du Golfe, De Witt and Robbins Is.). It is tempting to suggest that this distribution is due to a range expansion by this species near the time when the level of the sea was approaching its present level, and only the closer islands were still connected to mainland Tasmania.

By inspection of Table 4.1, it is possible to postulate a time for this expansion and a direction from which it came. For instance, *K. vulgaris* reached Schouten I., but apparently not Hunter I., although Schouten was cut off first. This species does not occur on Swan I. either, although that link to Tasmania was severed at about the same time as that to Maria I. If extinctions of *K. vulgaris* on offshore islands have not created a false impression, then this distribution corresponds to an expansion of the range of the species during the postglacial increase in rainfall

in the midlands and southern Tasmania between 11 500 and 6000 y BP as climates approached the "optimum" (Section 4.1). This expansion appears to have originated in the east. Unfortunately there are no published soundings for waters inshore of or between the islands of the Maatsuyker Group, so it is impossible to test this hypothesis with respect to the presence of *K. vulgaris* on only De Witt I. and Ile du Golfe. Other data, however, contribute interesting extensions to this discussion.

TABLE 4.1 Approximate severance dates for land links near Tasmania during most recent major rise of sea level. Information from Rawlinson (1974) and navigational charts.

Land Link	Depth of channel (m)	Date (y B.P.)
Craggy I. - Flinders I.	44	11 000
Clarke I. - Swan I.	31	9500
Swan I. - Tasmania	8	6250
Hogan Group - Wilsons Promontory	60	12 750
Hogan Group - Kent Group	60	12 750
Kent Group - Flinders I.	53	12 000
Robbins I. - Tasmania	2	5000
Hunter I. - Tasmania	10	7000
King I. - Tasmania	50	11 750
King I. - Cape Otway	80	14 750
Bruny I. - Tasmania	9	6750
Maria I. - Tasmania	7	6250
Schouten I. - Tasmania	18	7750

The absence of all (or all but one) of the eight eastern Bass Strait island species from the Tasmanian mainland is intriguing, especially as one of these species is found on Swan I., 3 km off the north-east coast. It is reasonable to expect that this species once occurred in what is now north-east Tasmania, leading to the suspicion that its absence now is

connected with the presence of *K. vulgaris* in that area. All species of *Keratroides* coexisting with *K. vulgaris* except perhaps *K. pyrensis* (about which habitat data are sketchy) occupy microhabitats which are distinctly different from the forest litter microhabitat of this widespread species. *K. albus* burrows deep in the soil of rainforests (Section 3.3), *K. angulosus* inhabits lower levels in the soil/litter profile than *K. vulgaris* (Chapter 7) and *K. rex* is found exclusively in backshore habitats, except on islands from which *K. vulgaris* is absent, where it occurs further inland. This evidence suggests that other *Keratroides* species cannot coexist in the litter with *K. vulgaris*, and that this may account for the absence of eastern Bass Strait *Keratroides* species, some of which appear to be litter dwellers, from the mainland of Tasmania.

None of the island *Keratroides* species are found in Victoria. A similar hypothesis may be advanced to explain this distribution, possible postglacial intrusives being *Arcitalitrus sylvaticus* and *Keratroides kershawi*.

If this suggestion is correct, then the eastern Bass Strait island species seem to have been well adapted to dry conditions by the end of the Late Wisconsin glaciation. They were apparently unable to compete with some species adapted to more mesic conditions, only persisting today in places protected by water barriers from invasion by the latter group.

The largest *K. angulosus* individuals collected in population samples from a study site in eastern Tasmania (Chapter 5-9) were females 9.0 mm long. *K. vulgaris* specimens found at the same place were up to 15.0 mm long. As explained in Chapter 7, a number of the ecological differences between the two species are to some extent related to this size difference. A ready mechanism for the evolution of niche segregation between two species is thus provided by the development of size difference. There is evidence to suggest that the small adult size of *K. angulosus* at the eastern study site is a consequence of its coexistence with *K. vulgaris*. Individuals of *K. angulosus* up to 11.0 mm long have been found in south coast populations (Table 4.2). The less frequent occurrence

of *K. vulgaris* in this area (Figure 4.17 c.f. e.g. Figure 4.9) combined with the isolation of these *K. angulosus* populations from others in Tasmania (Figure 4.16, Section 4.1), indicates that these south coast animals might represent the genotype present all over Tasmania before a very recent spread of *K. vulgaris*. If this hypothesis is correct, the findings in Chapter 7 indicate that *K. angulosus* was already occupying the subsoil habitat when *K. vulgaris* became sympatric with it, but that it was more active on the surface as well.

TABLE 4.2 Maximum lengths of *Keratroides angulosus* in collections from selected areas.

Locality	Length of largest specimen (mm)	No. of specimens examined
De Witt I.	11.0	51
Near Prion Beach, South Coast	10.0	75
Maatsuyker I.	9.5	49
Near Anglers Ck., eastern Tasmania	9.0	Thousands

Section 4.4 Discussion

Endemism of Tasmanian fauna

The Tasmanian landhopper fauna comprises fifteen species, of which only one is found on the mainland of Australia. In the discussion below, species occurring on the Tasmanian mainland but not on the Australian mainland (even if they exist on islands in Bass Strait) will be designated endemics. Thus the endemism of Tasmanian land amphipods, at the species level, is 93%.

The explanation of this very high rate of endemism is evident from earlier discussion; despite recent land connection, Bass Strait has for a long time been a barrier to the north-south movement of forest-dwelling landhoppers. During the last period of connection, this barrier was climatic, due to the aridity of the Bassian Isthmus, inhibiting exchange of desiccation-prone organisms. In this context, it is interesting to compare rates of endemism of the Tasmanian representatives of several groups of non-marine animals (Table 4.3). Only well-worked groups have been selected, with an emphasis on invertebrates from terrestrial and inland aquatic habitats. These groups have been subdivided according to their apparent vagility based on their habitats, powers of movement and physiological tolerances. This is obviously a subjective assessment, which may be made inaccurate by different ecologies of species within each group; however it is felt that the overall impression of vagility thus gained is a true one.

Rates of endemism correlate inversely with vagility quite closely. Apart from the molluscs, most of which can retreat into their shells, soil and litter dwellers show similar rates of endemism. The land planarians, however, show a much lower percentage of endemics than might be expected of slow-moving, cryptozoic animals with a low tolerance to dry conditions. This may result from their eggs being transported by man. Winsor (1977) designates a number of Victorian species "man-followers", as specimens are

TABLE 4.3 Rates of endemism amongst Tasmanian representatives of selected faunal groups.

Vagility	Group	No. of species in Tasmania	No. of species endemic to Tasmania	Percentage endemic to Tasmania	Authority
High to medium (good powers of movement, or very resistant stage).	Land mammals ¹	26	3	12%	Green, 1974
	Land birds ²	104	12	12%	Ridpath & Moreau, 1966
	Reptiles	15	3	20%	Rawlinson, 1974
	Anura	10	2	20%	Littlejohn & Martin, 1974
	Lepidoptera	32	3	9%	Couchman, 1977
	Coleoptera:				
	Dytiscidae	26	1	4%	Watts, 1978
	Odonata	27	5-6	19-22%	Allbrook, 1979
	Copepoda:				
	Calanoida (inland waters)	13	1	8%	Williams, 1974

Vagility	Group	No. of species in Tasmania	No. of species endemic to Tasmania	Percentage endemic to Tasmania	Authority
Low					
(restricted to a disjunct habitat but with moderate powers of move-- ment i.e. flight, or a resistant stage.	Trichoptera	157	116	74%	Neboiss, 1977
	Plecoptera	47	41-42	82-84%	Hynes & Hynes, 1980
	Gastropoda (terrestrial) ³	49	33	67%	Smith & Kershaw, 1979
Very low	Diptera:				
(strongly res-	Blephariceridae	6	6	100%	Zwick, 1977
tricted to a disjunct habitat, weak powers of movement, no resistant stage).	Coleoptera: Psephenidae	3	3	100%	J.A. Smith, p.c.
	Carabidae:				
	Trechinae: Trechini ⁴	63	62	98%	Moore, 1972, 1978
	Decapoda:				
	Parastacidae	9	7	78%	Various authors ⁵
	Amphipoda				
	Talitridae				
	(terrestrial)	15	14	93%	This study

Vagility	Group	No. of species in Tasmania	No. of species endemic to Tasmania	Percentage endemic to Tasmania	Authority
Very low	Isopoda:				
(cont'd)	Oniscoidea				
	(terrestrial)	31	25	81%	A.J.A. Green, p.c.
	Isopoda:				
	Phreatoicoidea ⁶	9	8	89%	Knott, 1975
	Syncarida:				
	Anaspidacea	8	7	88%	Various authors ⁷
	Oligochaeta:				
	Megascolecidae	48	48	100%	Jamieson, 1974
	Tricladida:				
	Geoplanidae	15	8	53%	Various authors ⁸

Notes:

1. Omitting bats and seals.
2. Omitting Clinking Currawong and Brown Scrub-wren from endemics, following Schodde (1975).
3. Tasmanian total includes only 3 non-retractable forms (slugs and semi-slugs).
4. A flightless group, including 4 troglodytic Tasmanian species.
5. Reik, 1969; Suter, 1977; Sumner, 1978.
6. Excluding hypsimetopids. Knott (1975) gives 7 endemics of a total of 8 in his Table 9.8, possibly omitting the only troglodytic species known from Tasmania.
7. Williams, 1974; Knott and Lake, 1980. *Koonunga cursor* has been found to occur in both Tasmania and Victoria (R. Swain, pers. comm.)
8. Fletcher and Hamilton, 1887; Dendy, 1890, 1893, 1894; Steel, 1901; Winsor, 1977.

often found in gardens and associated with agricultural practice.

Comparison of this rate of endemism with that of the landhoppers reinforces the assumption implicit in the above discussion that man's activity is unimportant in the distribution of Tasmanian amphipods.

The endemism of these Tasmanian groups is to some degree ecological, that is, due to the different requirements of the species and the different conditions prevailing on either side of Bass Strait. Tasmania is generally cooler and wetter than Victoria; sedgeland and alpine herbfield are either absent or at least floristically different in the mainland State. However, most Tasmanian forest habitat types are represented in Victoria, the wetter ones being found in southern mountains such as the Otway Range. The relatively low endemism present in the more vagile groups (Table 4.3) indicates that for the less vagile forest-dwelling groups at least, ecological differences do not make a large contribution to endemism. It is reasonable to assume that establishment might have occurred to a similar degree amongst the less vagile groups had Bass Strait not been such an effective barrier.

At the generic level, the endemism of Tasmanian landhoppers is much lower, four of the seven genera being found also on mainland Australia. Exchange of extant species between areas now forming the two mainlands and the smaller islands apparently occurred during the late Pleistocene (Section 4.4). Taken together with the degree of species endemism, the low generic endemism implies a substantial interchange of animals at a much earlier stage. This has already been discussed with respect to specific groups.

The world terrestrial amphipod fauna and its origins

Knowledge of the nature and distribution of the Tasmanian land amphipod fauna allows some extension of the discussion of the global fauna, reviewed in Section 4.1.

The high rate of endemism of this island's fauna has been indicated,

and attributed largely to the poor travelling ability of terrestrial amphipods. We may assume that a similar tendency towards endemism exists in all landhopper faunas. Most occurrences, therefore, must result either from previous land connections with a source area, or from development of terrestrial species from local supralittoral amphipods (which are better travellers).

The Tasmanian landhoppers show a strong relationship with the mainland Australian fauna, but bear little similarity to those of other parts of the world which have been reasonably well investigated. This applies particularly to New Zealand and Micronesia. A possible relationship between *Mysticotalitrus* and *Talitriator* (South Africa) has already been mentioned, but this was not investigated during the present study. The conclusion may be drawn however, that the Tasmanian fauna has been isolated from influences outside Australia for a long time. The most recent exchange with areas currently possessing landhopper faunas was probably before the separation of Africa from Antarctica, at about 90 My BP. Subsequent movement between Tasmania and Antarctica probably occurred until their separation, at about 55 My BP.

Examination of the distribution of Tasmanian genera reveals that those groups displaying most plesiomorphy (*Orchestiella*, *Tasmanorchestia* and *Austrotroides*) are restricted to the wetter western side of the island. In contrast it is noticeable that the more apomorphic genera (*Arcitalitrus* and *Keratroides*) are found, both in Tasmania and in mainland Australia, in drier situations. Although tolerance to desiccation may be enhanced by new morphological features developed, parallel changes in physiology, and probably behaviour, are implied. A further suggestion is that the ancestral landhoppers were inhabitants of very wet forest habitats, as mean annual rainfall in the west ranges between 1200 mm and 3200 mm (Figure 4.3).

The localities of all Australian collections examined during this study are shown in Figure 4.21. This includes material from a CSIRO survey of soil and litter fauna from about 600 sites all over Australia,

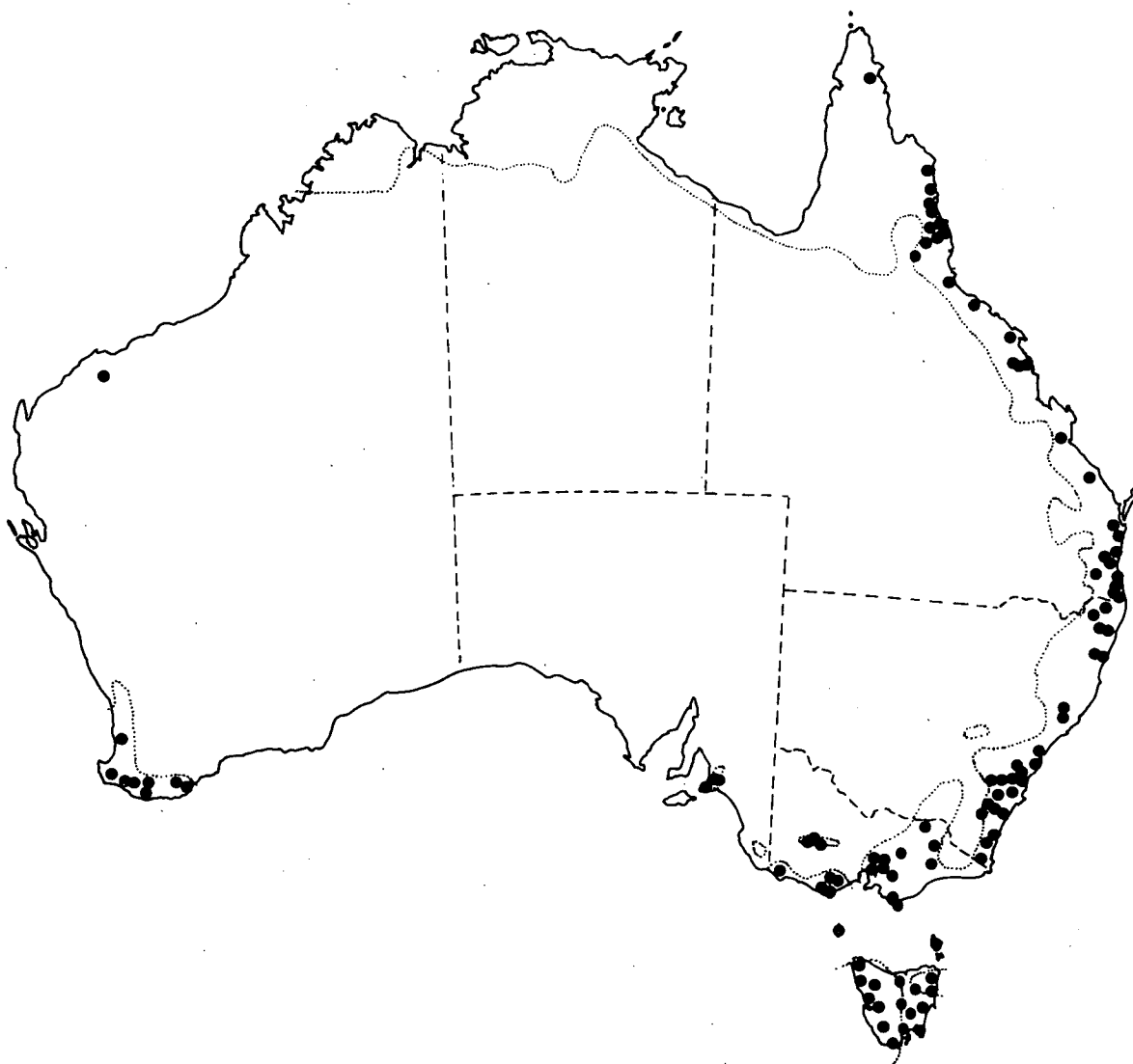


Figure 4.21 Localities of Australian collections of terrestrial amphipods examined. Dotted line represents the 760 mm (average annual precipitation) isohyet. Higher rainfall prevails on the coastal side of this line.

so it gives a fairly exhaustive coverage of the occurrence of landhoppers. Judging from this distribution, the climatic requirements of these animals appear to be as follows:

1) moderate to high rainfall (minimum of 600 mm annually; see Sandell, 1977. In the case of dry-adapted species, 500 mm; see Friend, in MS, Appendix)

2) No pronounced annual dry season, i.e. no period when no rain falls for several months

3) no ground-freezing frosts (see Bousfield, 1968).

The climatic classification used by Walter *et al.*, (1975) places the world's climates into ten categories occupying latitudinal zones as follows:

- I The equatorial zone
- II The tropical, summer rainfall zone
- III The subtropical dry zone
- IV The transition zone with winter rainfall
- The temperate zone, subdivided into areas with
- V Warm temperate climate
- VI Typical temperate climate
- VII Arid temperate climate
- VIII Cold-temperate or boreal climate
- IX The arctic zone
- X The mountain climate zone (non-latitudinal).

Amongst these broad categories, based on latitude, temperature and precipitation data, zone I and wetter areas of zones IV and V conform to the requirements listed above. Maritime areas of VI, where winters are mild, might also be included. The effect of mountain ranges is to increase precipitation and decrease evaporation on their slopes, and this tends to extend the suitable climatic conditions into otherwise unsuitable zones. Climate zones I, IV and V of Walter *et al.*, (1975) are plotted on the

world map in Figure 4.22. This corresponds well with the recorded distribution of land amphipods in the southern hemisphere (excluding South America). The coastal location of most of these areas appears to support Bousfield's (1968) suggestion that the ionic input to the ecosystem from onshore winds is necessary for landhopper survival. The present proposal, however, is that the maritime occurrence of the group is not due to this effect, but to temperature and precipitation conditions only.

The fact that the climate zones chosen above are, in reality, suitable for landhoppers is demonstrated by records of artificial introductions into areas without native faunas. These are marked on Figure 4.22 and include the following places:

Brazil	(de Castro 1972)
California	(Shoemaker, 1935; Mallis, 1942; Bousfield and Carlton, 1967)
Southern U.S.	(Shoemaker, 1935; Biernbaum, 1980)
W. Ireland	(Rawlinson, 1937)
Scilly Isles	(Hunt, 1925)
Cornwall	(Reid, 1947; Murphy, 1974, 1975; Richardson, in press).

The largest areas apparently possessing suitable climates, but in which native landhoppers have not been recorded are:

- a) western equatorial forests of Brazil and Colombia
- b) central coast of Chile and adjacent Andes
- c) southern Brazil
- d) equatorial west and central Africa
- e) valley of the Yangtze Kiang, China
- f) Spain and regions on northern coast of Mediterranean Sea
- g) California
- h) southern states of the eastern U.S.A.

The reality of apparent absences must be assessed in terms of the

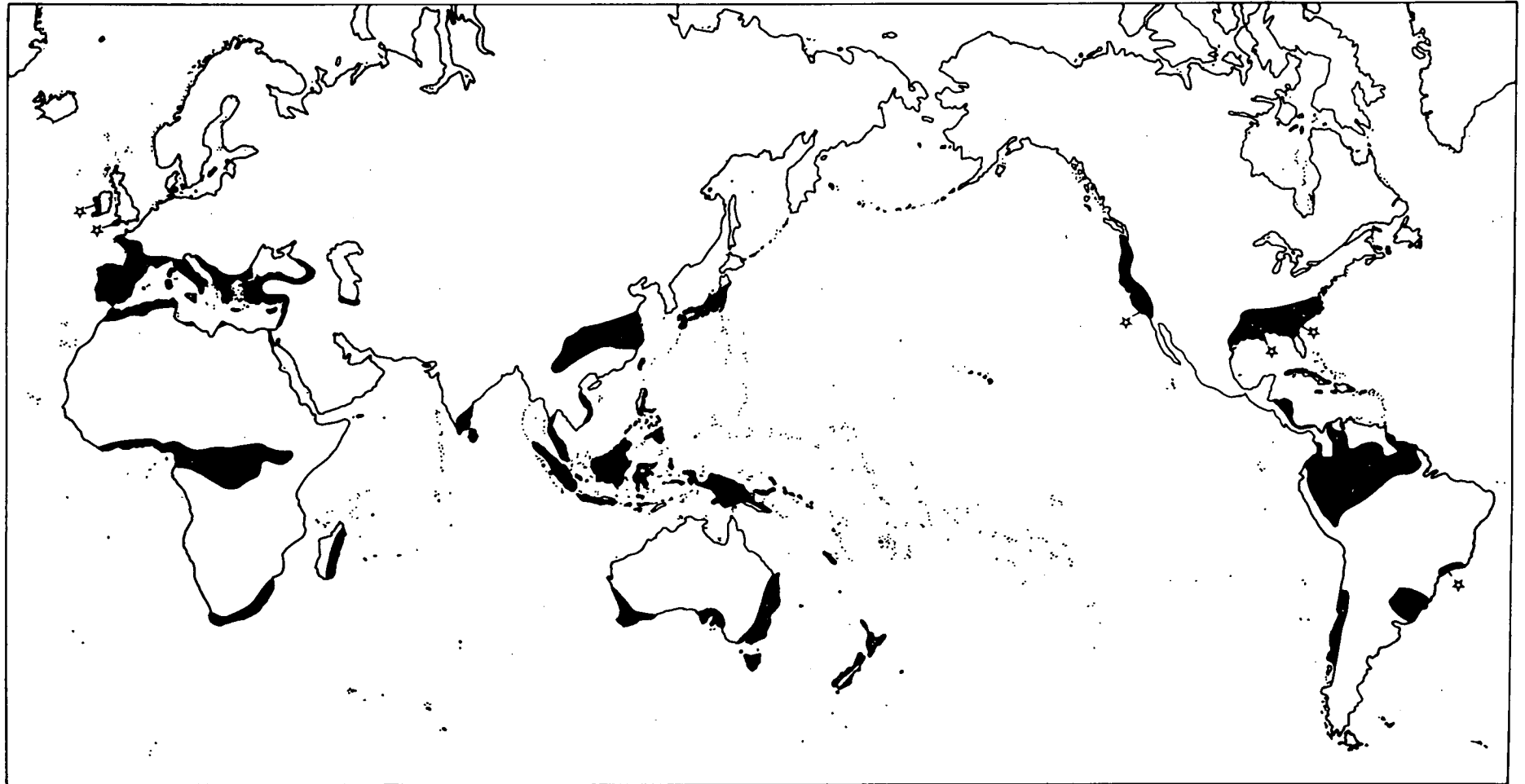


Figure 4.22 Climate zones I (equatorial), IV (Mediterranean) and V (warm temperate) of Walter *et al.* (1975), represented by black shading. Stars mark the recorded occurrence of terrestrial amphipods resulting from introductions to areas without native species.

development of scientific endeavour in various parts of the world. For instance, we can be fairly sure that the lack of records from Europe and North America (apart from introductions) is due to the genuine absence of terrestrial amphipods. In considering the other areas, however, we cannot be as certain. The case of South America has already been considered (Section 4.1). Little work has been published on the cryptozoa of equatorial Africa. Madge (1965) gave a list of litter fauna present in tropical forest in Ibadan, Nigeria, which did not include amphipods; however, his rainfall data showed a pronounced dry period from November to February. Ibadan is some way inland and on the edge of the equatorial climate belt in Figure 4.22. In this context it is interesting to note the record of "*Talitrus gulliveri*" (Ruffo, 1949b) from Annobon, an island in the Gulf of Guinea. Perhaps further investigation would reveal the presence of landhoppers on the African coast in this area.

Similarly, it is difficult to know whether the lack of Chinese records indicates an absence of amphipods, in the light of occurrences in north-west Assam (Tattersall, 1914) and northern Burma (Barnard, 1935). Luzon (Baker, 1915) and Japan (Iwasa, 1939) both have amphipod faunas, and it is reasonable to expect that Taiwan supports one, although there is no such record in the literature.

Despite this uncertainty, the fact emerges that very few areas of the former Laurasian supercontinent have landhoppers today. The world fauna is dominated by elements (including most of the sexually similar species) riding on Gondwanaland fragments.

Bousfield (1968) suggested an origin of sexually similar species on Gondwanaland, and of sexually dimorphic species locally from supralittoral talitrids. By correlating the development of gnathopod form with other peculiarly terrestrial features, it has been indicated that a tendency exists for sexually similar gnathopods to develop with other apomorphic features from the plesiomorphic, sexually dimorphic shore-

hopper facies (Chapter 3). It is postulated that the appearance of these features is a function of time since the invasion of land by the amphipod ancestral to the species concerned, and that successful invasions have occurred repeatedly.

Thus the older lines (sexually similar species) show a Gondwanaland distribution (except for South America, so far) while those from more recent invasions exist in some other parts of the world where climates are suitable. It is suggested that when the progenitors of the earlier lines invaded the land, supralittoral talitrids existed only in Gondwanaland, which was still complete, or nearly so. Since the breakup of that super-continent and the collision of some of its components with Laurasian fragments, supralittoral talitrids have spread around the coasts of the northern continents. The northward-moving pieces of Gondwanaland had to pass through the "horse latitudes" of seasonal dryness, which have existed since Miocene times (Kemp, 1978), before colliding with Laurasian fragments. While the shore-dwelling species could survive this, terrestrial species could not, so landhopper faunas were rarely transported to the northern continents. A record of a sexually similar species from northern Burma (Barnard, 1935) may be the result of such a transfer, from the Indian plate to southern Asia.

In Laurasian areas where climates are suitable, landhoppers have arisen recently from the local shore-hoppers, and are represented by sexually dimorphic species such as those found in Japan, Indonesia and the Canary Is. The lack of these recent terrestrial species from suitable areas of North America, western Asia (Black Sea coasts) and Europe may be related to the greater severity of Pleistocene glacial climates on the larger northern continents. Thus the modern landhopper fauna appears to be the result of a limited number of different invasions of the land, occurring from before the breakup of Gondwanaland until the present day. Many extinctions of terrestrial lines must have occurred, leaving a limited number of well-established older groups and a greater number of more recent

groups showing restricted distributions. It is probable that these invasions were all due to members of an old *Orchestia*-type lineage which also gave rise to the various modern beach-hopper groups (see Chapter 2).

The origin of the supralittoral Talitridae in Gondwanaland suggests that the radiation of the Talitroidea occurred there. This is further supported by the distribution of the freshwater Hyalellidae. *Afrochiltonia* occurs in South Africa, *Austrochiltonia* in Australia, *Chiltonia* in New Zealand and Campbell I. and *Hyalella* in South America, with *H. azteca*, *H. texana* and *H. montezumana* extending its range into North America. The terrestrial Talitridae and the freshwater Hyalellidae are the only non-marine members of the Talitroidea, and thus are the only groups which might be expected to provide evidence for a Gondwana radiation of this superfamily.

Following the arguments above, the occurrence of an apomorphic species in Jamaica (Hurley, 1959) is evidence of Gondwanaland faunal elements there. This further indicates the presence of an old landhopper fauna in South America. Further collection and description of terrestrial amphipods is necessary before the validity of these hypotheses can be fully assessed.